1573294

1
Ag84Ah

United States
Department of
Agriculture

Science and
Education
Administration

Agriculture
Handbook
Number 552

cop. 5

The Yellowjackets of America North of Mexico

U.S.D.A.
NAT'L AGRIC LIBRARY
RECEIVED
APR 1 18
PROCUREMENT SECTION
CURRENT SERIAL RECORD

United States Department of Agriculture

Science and Education Administration

Agriculture Handbook Number 552

The Yellowjackets of America North of Mexico

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington, D.C. 20402

ABSTRACT

Akre, R.D., A. Greene, J.F. MacDonald, P.J. Landolt, and H. G. Davis. 1980. Yellowjackets of America North of Mexico. U.S. Department of Agriculture, Agriculture Handbook No. 552, 102 pp.

This volume is a compendium of data on the pestiferous vespines (hornets and yellowjackets) of the United States and Canada. Sections cover taxonomy, biology, economic and medical importance, and control. Illustrated keys are included for rapid identification of species, and a glossary defines many of the unusual terms used in the text.

Keywords: Hymenoptera, Vespinae, *Vespa*, *Vespula*, *Dolichovespula*, yellowjackets, hornets, yellowjacket biology, economic losses, stings, sting reactions, yellowjacket keys, control, urban problems

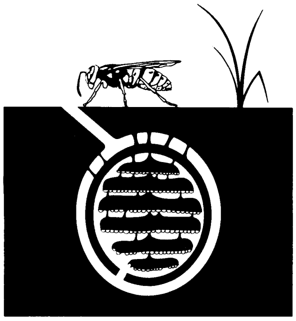
This publication reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate State and/or Federal agencies before they can be recommended.

CAUTION: Pesticides can be injurious to humans, domestic animals, beneficial insects, desirable plants, and fish or other wildlife—if they are not handled or applied properly. Use all pesticides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and pesticide containers.

Trade names are used in this publication solely to provide specific information. Mention of a trade name does not constitute a warranty or an endorsement of the product by the U.S. Department of Agriculture to the exclusion of other products not mentioned.

Issued June 1981

CONTENTS



The Yellowjackets of America North of Mexico

BY

ROGER D. AKRE, *entomologist*, Department of Entomology, Washington State University, Pullman, Wash.

ALBERT GREENE, *research associate*, Department of Entomology, University of Maryland, College Park, Md.

JOHN F. MACDONALD, *assistant professor*, Department of Entomology, Purdue University, West Lafayette, Ind.

PETER J. LANDOLT, *research assistant*, Department of Entomology, Washington State University, Pullman, Wash.

HARRY G. DAVIS, *entomologist*, U.S. Department of Agriculture, Science and Education Administration, Yakima, Wash.

INTRODUCTION

This handbook was written in response to a growing need for a general manual on identification, biology, and control of North American yellowjackets. With the continually increasing popularity of outdoor recreational activities, more and more people are becoming familiar with these abundant, brightly colored, moderately large to large wasps, possessing a fiery sting seemingly all out of proportion to their size. The persistence of some species in partaking of both our food and our garbage, as well as the construction of many nests in locations with a high probability of accidental and unfortunate human discovery, often result in a pest status that ranges from mild nuisance to severe hazard.

All true wasps belong to the order Hymenoptera (along with ants and bees), and have a fully developed sting. Of the 4,000 wasp species in the United States (Evans and Eberhard, *1970*)[1] and 15,000 in the world (Hurd, *1955*), most are solitary and inoffensive insects that use their sting to paralyze their arthropod prey. Fully social (eusocial) behavior in wasps is limited almost exclusively to the family Vespidae, whose members use their sting primarily for defense. The most advanced social organization in this family is found in the subfamily Vespinae, which includes the yellowjackets and hornets.

The term "yellowjacket" seems to be of American origin (Europeans simply call them wasps). It properly refers to all members of the genera *Vespula* Thomson and *Dolichovespula* Rohwer, although several of these insects are white and black rather than yellow and black, and two northern species are also marked with red. They are nearly ubiquitous throughout North America with the exception of the major desert areas and the uppermost latitudes with very cool summers of 6° to 10°C (43° to 50°F) during the warmest month (fig. 1). True hornets are closely related but are much larger Old World wasps in the genus *Vespa* L.; one introduced species occurs in eastern North America, and is included in this handbook.

It is small comfort to know that not only man, but other animals have problems with vespine wasps, as the following passage from Corbett (*1955*) makes clear: "On reaching the kill the tiger started blowing on it. In the Himalayas, and especially in the summer, kills attract many hornets, most of which leave as the first light fades but those that are too torpid to fly remain, and a

[1]The year in italic, when it follows the author's name, refers to Literature Cited, p. 94.

tiger—possibly after bitter experience—blows off the hornets adhering to the exposed portion of the flesh before starting to feed." During a 1973 outbreak of yellowjackets in the Pacific Northwest, great masses of the wasps alighted on both human and animal food in the Portland, Oreg., zoo. The lions and tigers were particularly affected, receiving multiple stings about the mouth and refusing to feed for 4 to 6 hours.

What may be the first mentions of human contact with vespines are references to fear of hornets by Middle Eastern peoples in the Old Testament of the Bible. "Even today, the hornet in the Middle East is a pest to be feared, their

FIGURE 1 — Map of North America showing areas of very cool summers with the mean temperature of the warmest month 6° to 10°C (43° to 50°F). Yellowjackets seldom occur in these areas. Also shown are desert areas and mountain ranges, which influence vespine occurrence and distribution.

ravages of fruit crops and honeybee colonies making horticulture and agriculture at times difficult, at other times virtually impossible" (Spradbery, *1973*a). As this handbook will demonstrate, yellowjackets in North America are no less an economic problem. In the early 1960's, the U.S. Department of Agriculture (USDA) received 10,000 requests per year for information on these wasps (Fluno, *1961*), and the number today is probably far greater. Yellowjackets are responsible for dramatic drops in park, campground, and resort attendance, curtailment of logging operations, and the impairment of both fruit harvesting and forest fire fighting. Yellowjackets probably cause far more than the reported 15 to 20 deaths per year in the United States, because the symptoms of a serious allergic reaction to stinging are extremely similar to those of heart attacks and are undoubtedly often mistaken as such.

The unsavory reputation of yellowjackets is therefore, well-deserved, and in many cases justifies control measures (although the methods currently available often fail to deal adequately with the problem). This handbook, however, will emphasize the paradox that yellowjackets are also beneficial insects, which appear to be key factors in the natural control of many pestiferous insects. Lastly, it is hoped this work will stimulate interest in yellowjackets for their own sake, as some of our most fascinating and dynamic insect fauna.

LITERATURE REVIEW

A world list of literature useful to researchers on yellowjacket biology was published by Akre et al. (*1974*). The 717 entries were coded as to contents. Other useful references are the books on wasps by Kemper and Döhring (*1967*) (in German), Evans and Eberhard (*1970*), Guiglia (*1972*) (in French), and Spradbery (*1973*a). The Kemper and Döhring and Guiglia references contain information only on vespids, whereas the other two references also include information on other families of wasps. Three additional authors with chapters or sections on wasps (including yellowjackets) are Ebeling (*1975*), Iwata (*1976*) and Wilson (*1971*). The Iwata reference summarizes information on many species of Far Eastern wasps previously available only in Japanese.

Akre and Davis (*1978*) reviewed the ecology and behavior of the Vespidae, while Davis (*1978*) reported on problems caused by yellowjackets in the urban environment. MacDonald et al. (*1976*) discussed the status of yellowjacket control programs in the United States. All other literature on yellowjacket biology is concerned with individual species or specific investigations.

TAXONOMY

Introduction

The family Vespidae formerly included the subfamilies Masarinae, Eumeninae, and Vespinae (Bequaert, *1918*; Bradley, *1922*), which have since been elevated to family rank (Brothers, *1975*; Richards, *1962*). They now constitute the three families of the Vespoidea. Vespoid wasps are recognized by the elongate discoidal cell in the forewing and the longitudinal folding of the wings at rest (with the exception of most Masaridae). Members of all three vespoid families are found in North America, although most human contact is with the social Vespidae. Vespidae and Eumenidae are distributed transcontinentally, whereas Masaridae are found in the Western United States and southwestern Canada.

Most Masaridae are solitary, yellow and black wasps that provision their mud cells with pollen and nectar rather than arthropod prey. They are easily separated from other Vespoidea by clubbed antennae and the presence of two, rather than three, submarginal cells in the forewing. Masarids are relatively scarce in most localities and rather innocuous.

Eumenidae, also solitary and harmless to humans, are predaceous and make a variety of nest types in soil, in twig cavities, or on various surfaces. They are recognized by a combination of characteristics: Middle tibiae with one apical spur, toothed or bifid tarsal claws, filiform antennae, and three submarginal cells in the forewing.

The Vespidae, consisting of the subfamilies Stenogastrinae, Polistinae, and Vespinae, have two apical spurs on the middle tibiae, simple tarsal claws, and three submarginal cells in the forewing. The stenogastrines are found only in Southeast Asia (fig. 2). Their small colonies are found in deep forests, and most species are presocial (Spradbery, *1975*). Van der Vecht (*1977*) discussed the phylogeny and taxonomic status of the Stenogastrinae and tentatively concluded they should either be a separate family or a subfamily of Eumenidae.

The Polistinae are eusocial wasps. This subfamily includes the large and diverse tribes, Ropalidiini and Polybiini, and the monotypic tribe that contains the cosmopolitan genus *Polistes* Latreille (Polistini). Richards (*1978*) revised the American species and subspecies of Polistinae and summarized information on their biology. The Ropalidiini are found only in Africa and Australasia (fig. 3). The Polybiini are primarily Neotropical (23 genera), with three additional genera found in Africa and Asia, and four (or possibly six) species distributed into temperate latitudes in North America (fig. 4).

Mischocyttarus flavitarsis (Saussure) is found in the Western United States and into southern British Columbia. It is similar in appearance to *Polistes* but can be readily distinguished by the narrow, stalklike first gastral segment. Nests are small and similar in architecture to *Polistes* nests. Like *Polistes*, these wasps may be found hibernating in large numbers in buildings and attics of houses. A related species, *M. cubensis*

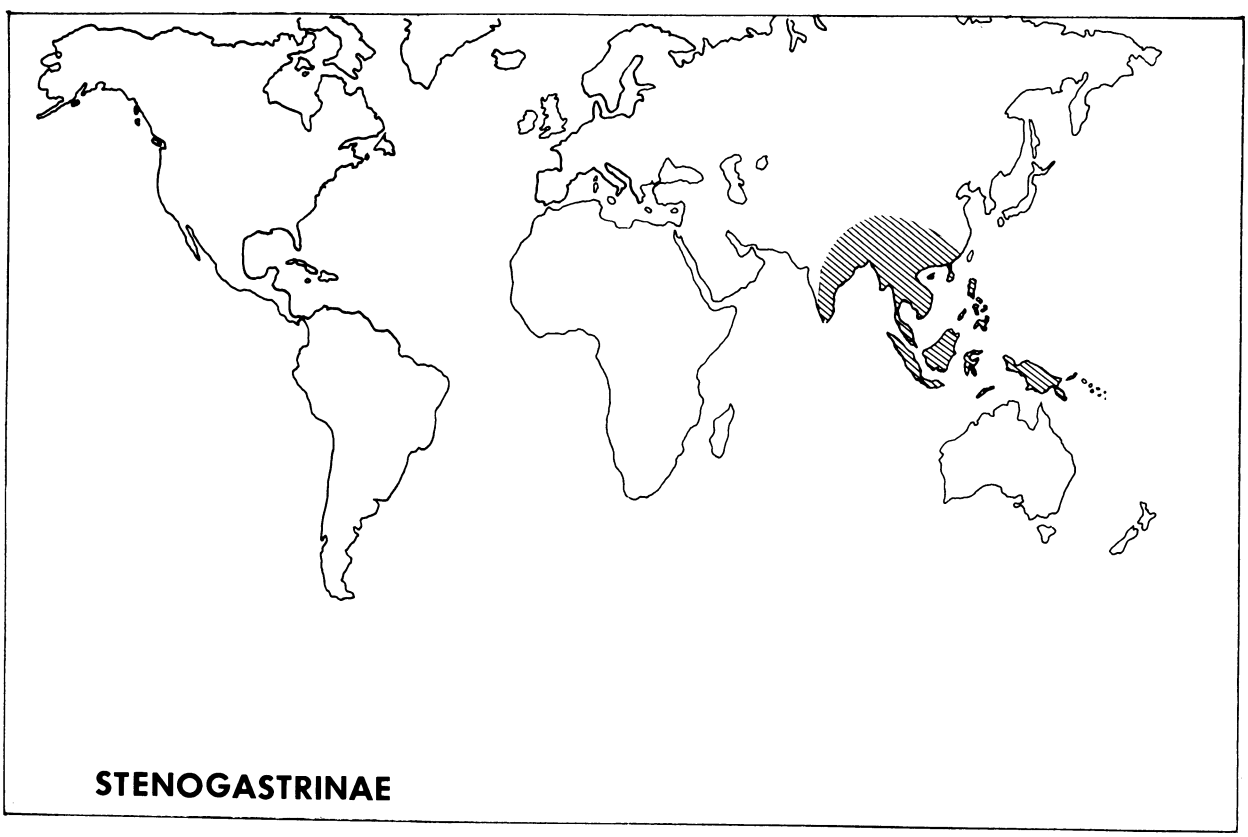


FIGURE 2 — Distribution of Stenogastrinae (drawn by G. Shinn).

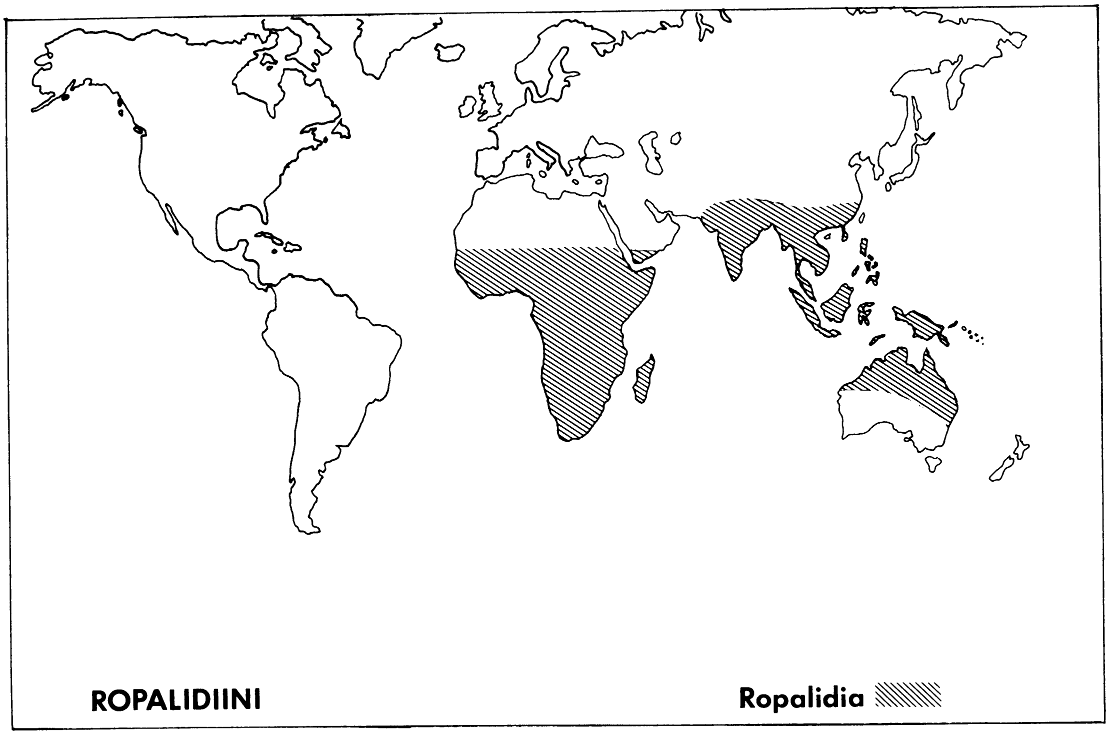


FIGURE 3 — Distribution of Ropalidiini (G. Shinn).

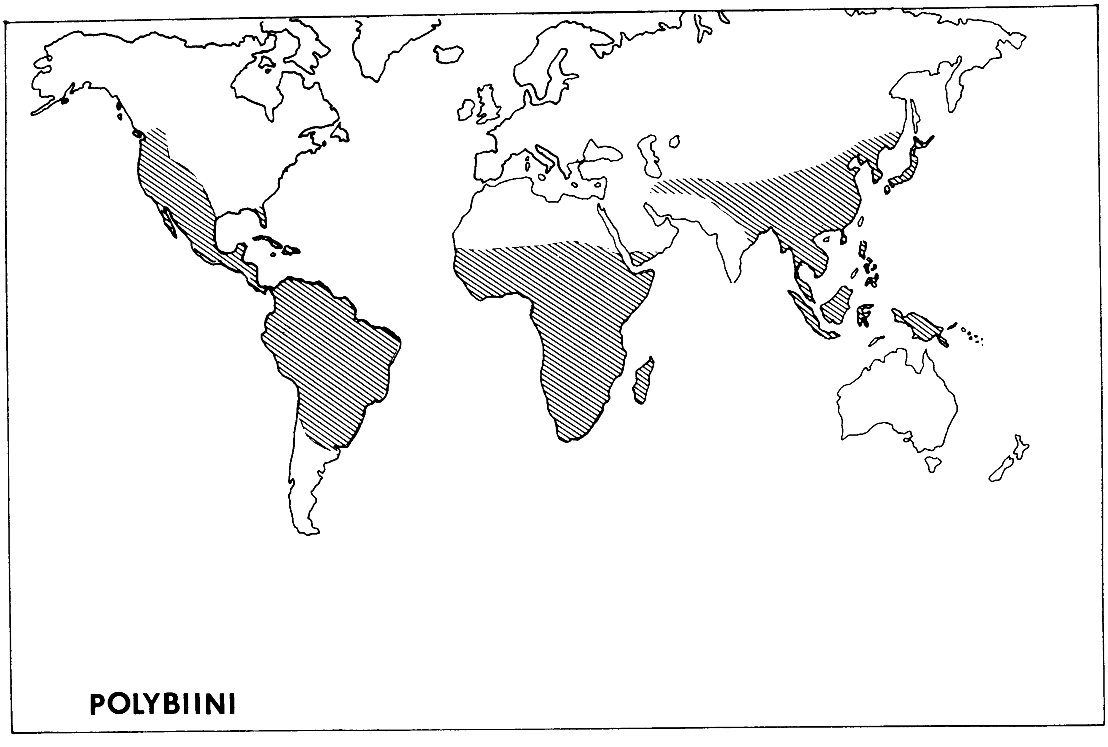


FIGURE 4 — Distribution of Polybiini (G. Shinn).

(Saussure), occurs from Florida to South Carolina, whereas *M. mexicanus* (Saussure) occurs in southern Texas. (Richards, *1978*, raised *M. cubensis mexicanus* to species level.)

Brachygastra mellifera (Say) has a Neotropical distribution but also extends north into southern Texas and Arizona. Their large and populous paper nests are comprised of concentric combs covered by a single paper envelope (Bequaert, *1933*). They are known for their honey-storing behavior. In addition, two species of *Polybia* have been collected (or intercepted in quarantine) at Nogales, Ariz., on the U.S. border.

Polistes (paper wasps) occur throughout most of the world (fig. 5). They make a single, usually horizontal, comb with no surrounding envelope. Colonies are founded in spring by one or more overwintered females. One female becomes the dominant queen and egg layer while the remainder function as subordinate workers (Pardi, *1948*). Emerging females are workers until later in the season when reproductives are produced. Colony size is small with usually less than 200 adults reared through the season. More detailed accounts were given by Evans and Eberhard (*1970*), West Eberhard (*1969*), and Wilson (*1971*). Paper wasps are generally not pests unless the nest is disturbed or large numbers of females, looking for suitable overwintering sites, find their way into buildings in autumn. Their predatory habits, especially on caterpillars, make them beneficial to gardeners and farmers.

The Vespinae (*Provespa* Ashmead, *Vespa*, *Vespula*, *Dolichovespula*) occur throughout the Northern Hemisphere and in Southeast Asia (fig. 6). The three species of *Provespa* are found only in Southeast Asia and are nocturnal (van der Vecht, *1957*). *Vespa* is primarily eastern Asian with two species, *Vespa orientalis* Fab. and *V. crabro* L., found in the western Palearctic. *V. crabro* has also been introduced into the Eastern United States. In this handbook, the yellowjackets are considered to belong to two distinct genera, the generally ground-nesting *Vespula*

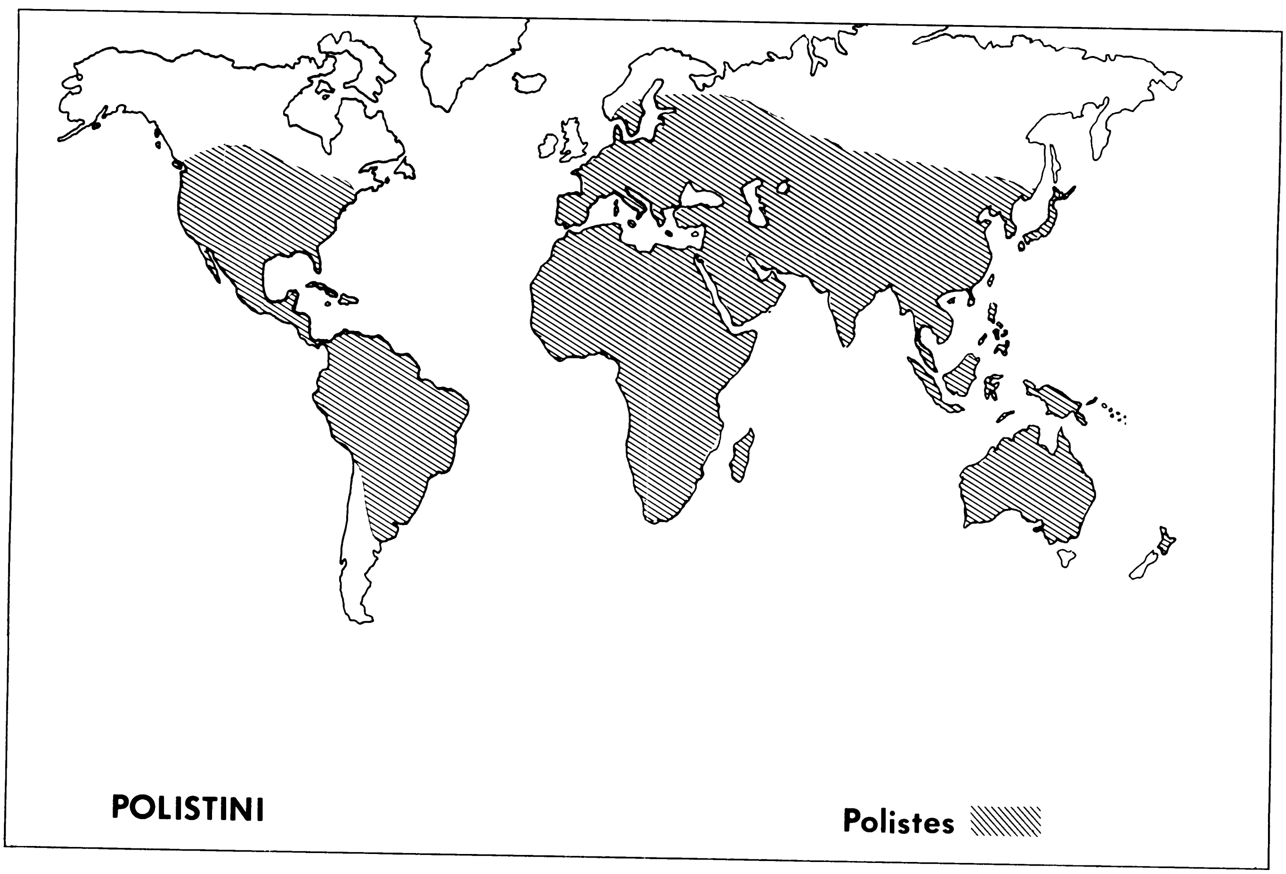


FIGURE 5 — Distribution of Polistini (G. Shinn).

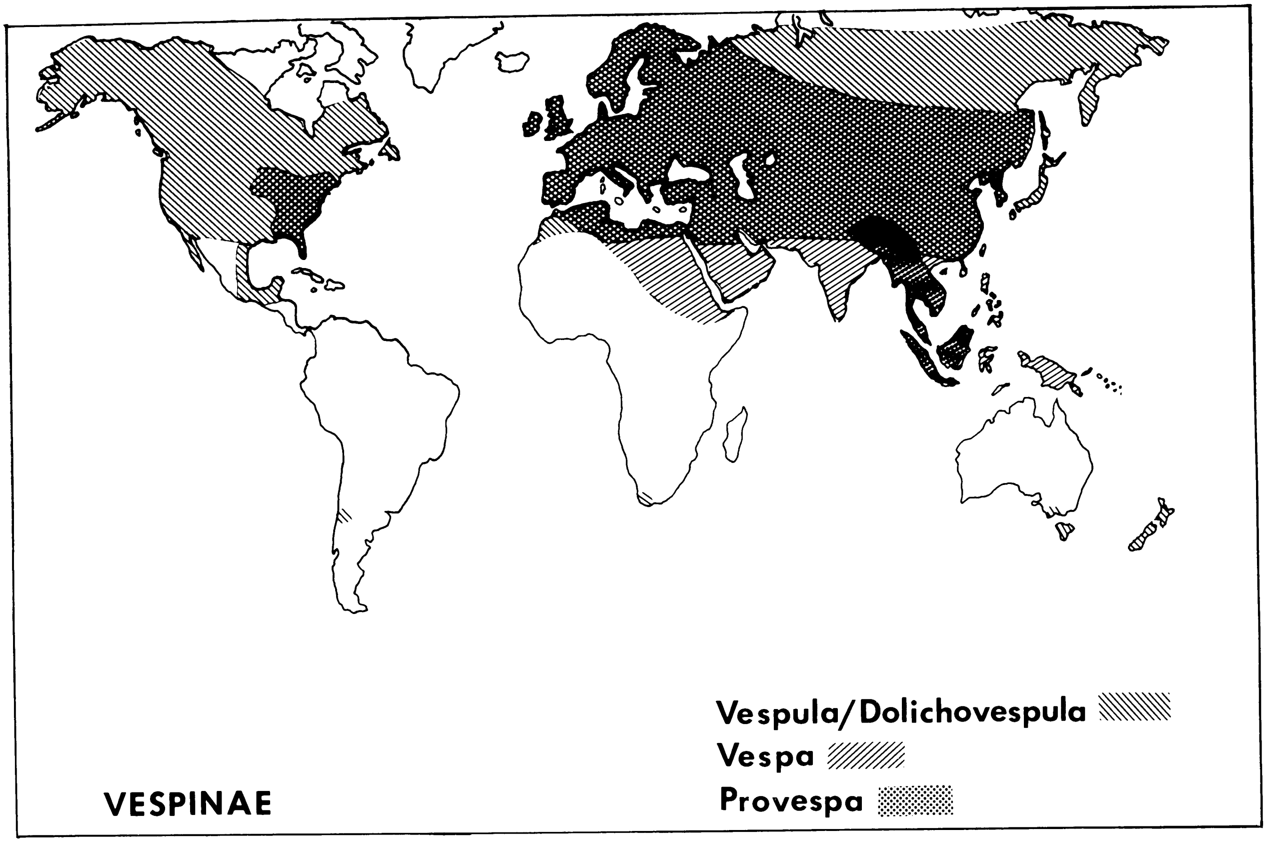


FIGURE 6 — Distribution of Vespinae (G. Shinn).

and the generally aerial-nesting *Dolichovespula*. Both are Holarctic. In addition, *Vespula germanica* (Fab.), a European species, has been introduced into New Zealand, Australia, South Africa, and Chile, as well as the Eastern United States (Edwards, *1976*). *Vespula vulgaris* (L.), a Holarctic species, has been introduced into Australia (Spradbery, *1973b*).

Identification of Genera and Species

Worker yellowjackets are fairly small wasps about 10 to 14 mm (1/2 inch) long (fig. 7*a*) and are strikingly marked with black and yellow or black and white patterns. In the United States, the term "hornet" is generally applied to two much larger species in the same subfamily (*Dolichovespula maculata* (L.), *Vespa crabro*), and sometimes to all aerial-nesting yellowjackets. Technically, however, only species in the genus *Vespa* (of which *V. crabro* is the only North American example) are hornets.

Although the Vespinae are a well-defined and easily recognized group, they are often confused with paper wasps in the genus *Polistes*. Paper wasps can be readily distinguished by their elongate legs and larger, more slender bodies (fig. 7*b*). Their nests always consist of a single, exposed comb (fig. 8*a,b*), suspended by a narrow stalk and often located under eaves, porches, or other manmade structures. Yellowjacket nests, even very young ones, have a globular or oval paper envelope that usually encloses multiple combs (fig. 9).

The following pictorial key will serve to identify workers of the 16 species of free-living yellowjackets and the single species of hornet found in North America. (Two parasitic yellowjackets, *Dolichovespula arctica* (Rohwer) and *Vespula austriaca* (Panzer), do not have a worker caste, and utilize workers of the host species to care for their own brood). Figure 10 illustrates those structures referred to in the key. Except for the recognition of *Vespula* and *Dolichovespula* as

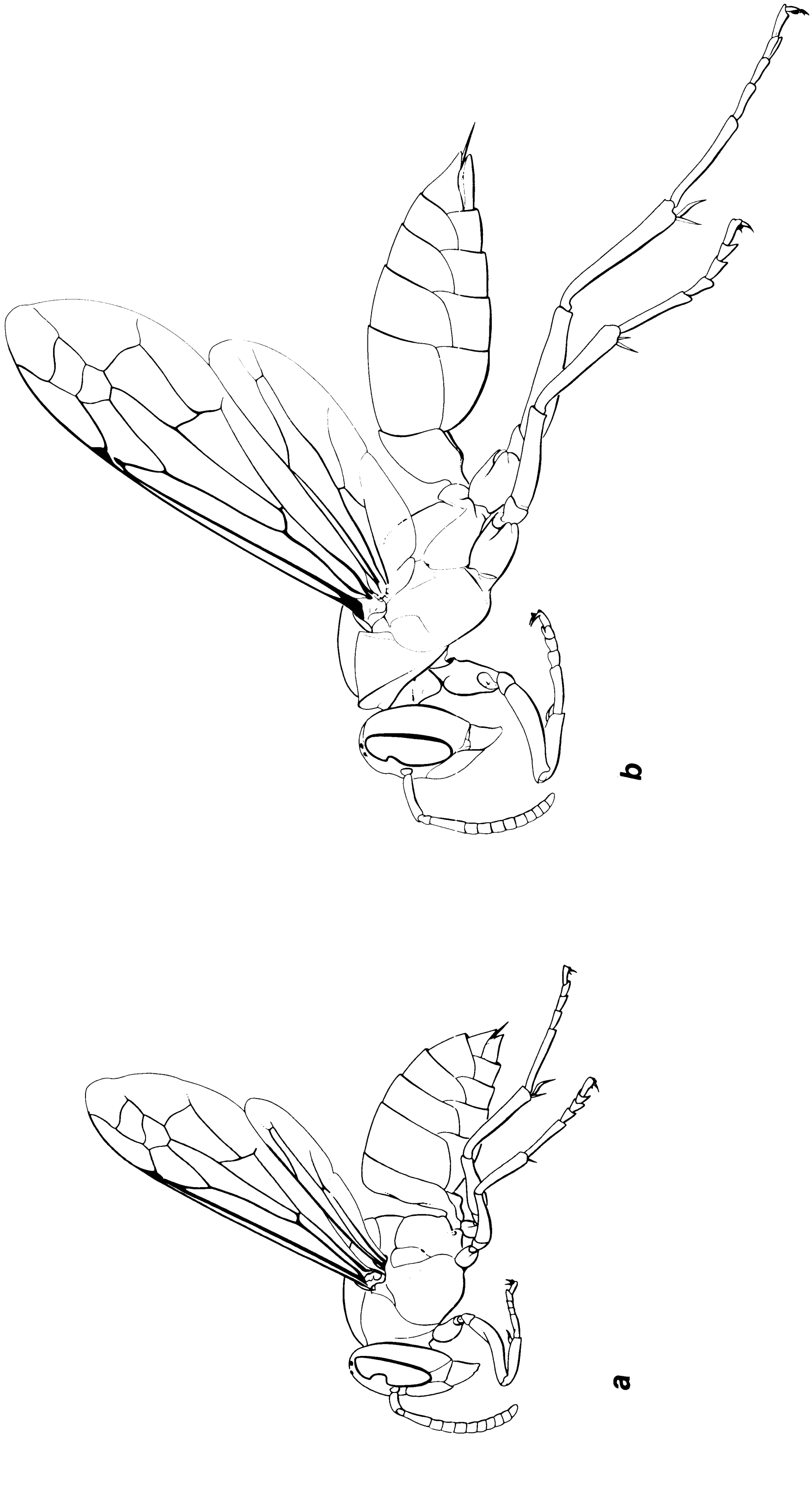
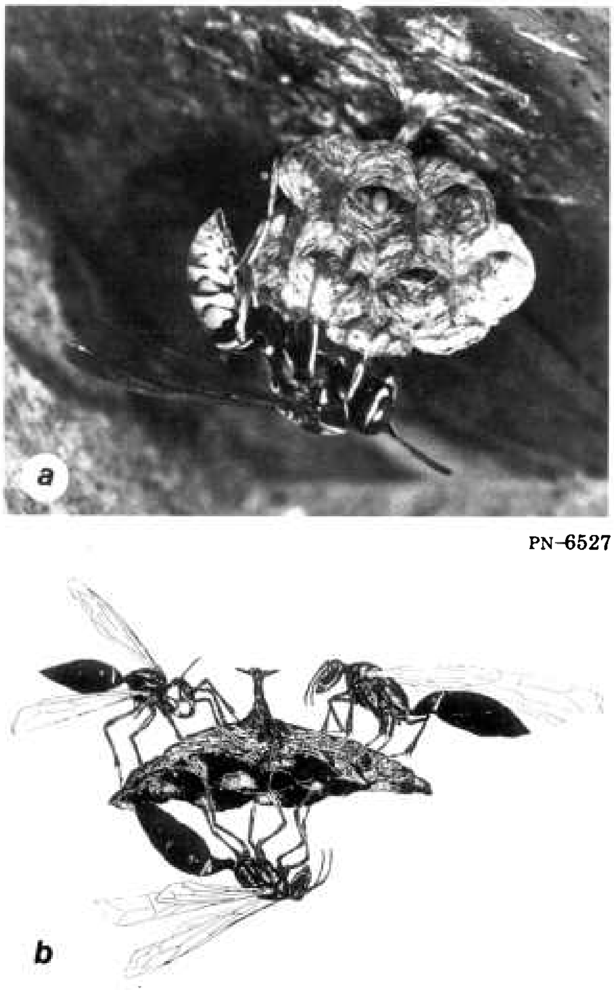


FIGURE 7 — *a*, Yellowjacket worker; *b*, female *Polistes*, both illustrations drawn without color patterns.

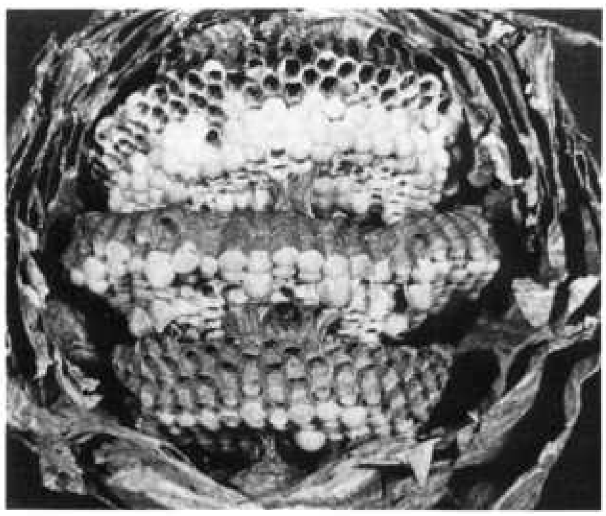


PN-6527

FIGURE 8 — *a*, *Polistes* queen on her nest; *b*, *Polistes* nest showing single, exposed comb (J. Krispyn).

separate genera, the taxonomic treatment of Miller (*1961*) has been followed. Most species are quite distinct and often can be determined on the basis of gaster color pattern alone; however, since these markings always vary to some degree and may appear similar in some closely related species, identifications should always be made on a series of specimens when possible. Two sources of confusion are commonly encountered: (1) The color patterns of worker *Vespula acadica* (Sladen) and *V. atropilosa* (Sladen) vary widely and often bear a superficial resemblance to each other. A complete range of patterns may be found within one colony, although certain colonies tend to produce either xanthic (very yellow) or melanic (very black) individuals. (2) Similarly, yellowjacket identification in eastern North America is complicated by the fairly close resemblance of four species, all of which may occur in some areas: *Vespula vulgaris, V. maculifrons* (Buysson), *V. germanica*, and *V. flavopilosa* Jacobson.

Until recently, only the first three species were recognized, with the differences between them elaborated in detail in Menke and Snelling (*1975*); however, morphological, biological, and electrophorectic studies have now revealed a previously unrecognized form, *V. flavopilosa*, which has long been confused with the closely related *V. vulgaris* and *V. maculifrons* (Jacobson et al., *1978;* figs. 10, 11, and 16 of Menke and Snelling, *1975*, labeled *V. maculifrons*, are *V. flavopilosa*). Much of this confusion was due to the large amount of color pattern dimorphism that exists between *V. flavopilosa* queens and workers, making asssociation of individually collected females difficult. For instance, *V. flavopilosa* queens sometimes closely resemble those of *V. vulgaris*, whereas the gasters of highly xanthic *V. flavopilosa* workers may be practically indistinguishable from those of melanic *V. germanica*. Examination of *V. flavopilosa* from over 25 nests, however, revealed stable color patterns among females and males both within and among all colonies examined from Georgia, North Carolina, Pennsylvania, and New York. In addition, comparative electrophoretic studies showed consistent enzymatic differences between *V. flavopilosa* and the three



PN-6528

FIGURE 9 — Nest of *Dolichovespula maculata* with half of envelope removed to expose the multiple combs.

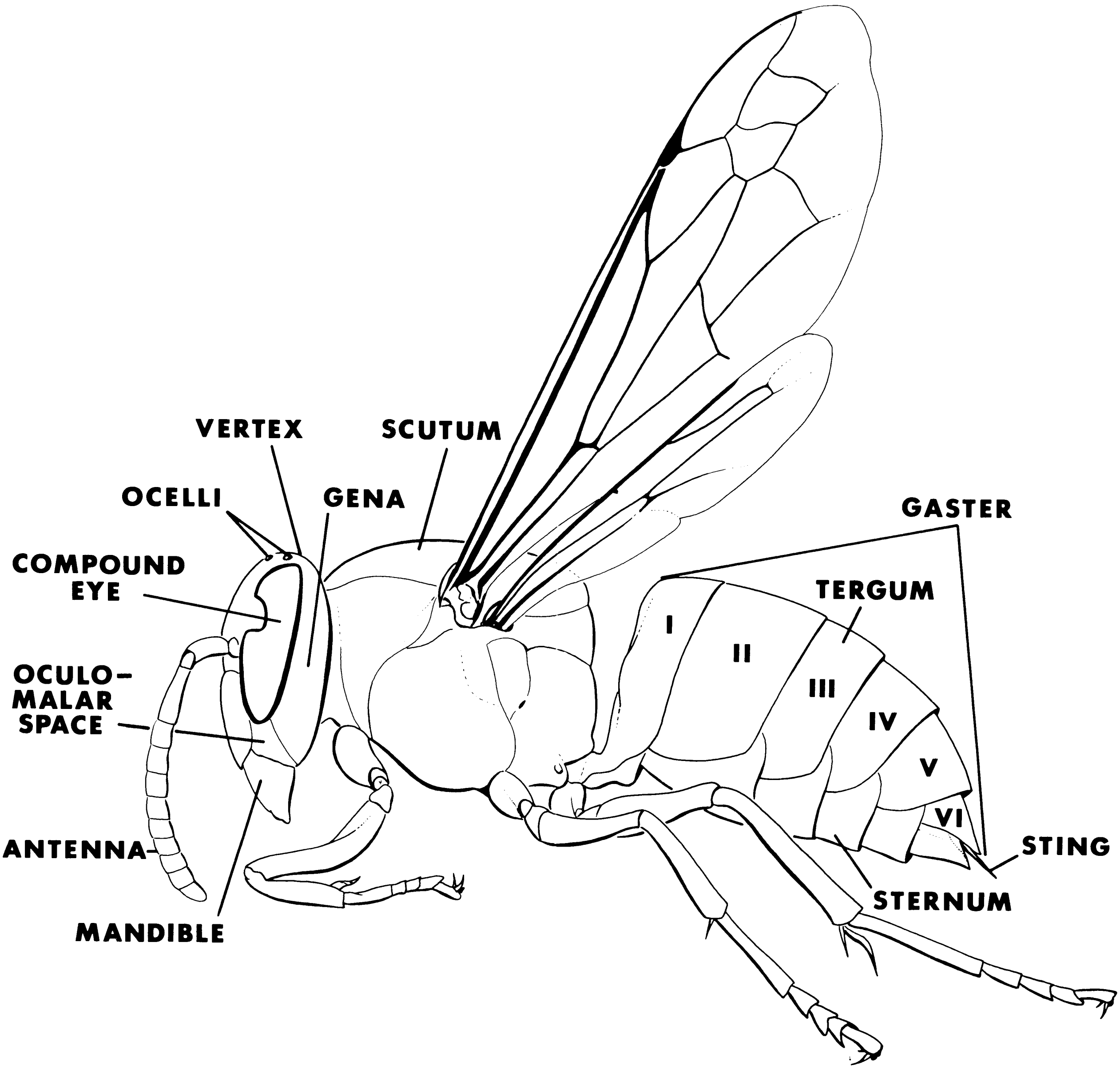


FIGURE 10—Worker yellowjacket illustrating structures used in the key, pages 12 to 22.

eastern species of the *V. vulgaris* group as well as a western member, *V. pensylvanica* (Saussure) (Jacobson et al., *1978*). *V. flavopilosa* maintains its identity sympatrically (occurring in same geographical area) with *V. maculifrons* throughout its range, and with *V. vulgaris* and *V. germanica* in its northern distribution. Since *V. flavopilosa* could conceivably be a hybrid between *V. maculifrons* and *V. vulgaris* (and most likely arose as such), it is significant that *V. flavopilosa* exists farther south than the apparent southernmost distribution of *V. vulgaris* in the Eastern States.

Since the key was constructed, Wagner (*1978*) presented evidence to show that *Dolichovespula saxonica* (Fab.), previously considered Palearctic, is widely distributed in the Nearctic. This species (as defined) is closely related to, and easily confused with, *D. norvegicoides* (Sladen). As part of the evidence, he reported on two colonies, one with a nest in a wall void at King's Mountain, Alaska; the other a supraterrestrial (on the surface of the ground in a hollow cavity) nest at Eagle River, Alaska. No collection dates were given for either colony. The first nest was reported to have a tiered envelope similar to nests of *D. saxonica* in Europe, whereas the second nest had an interconnecting envelope that

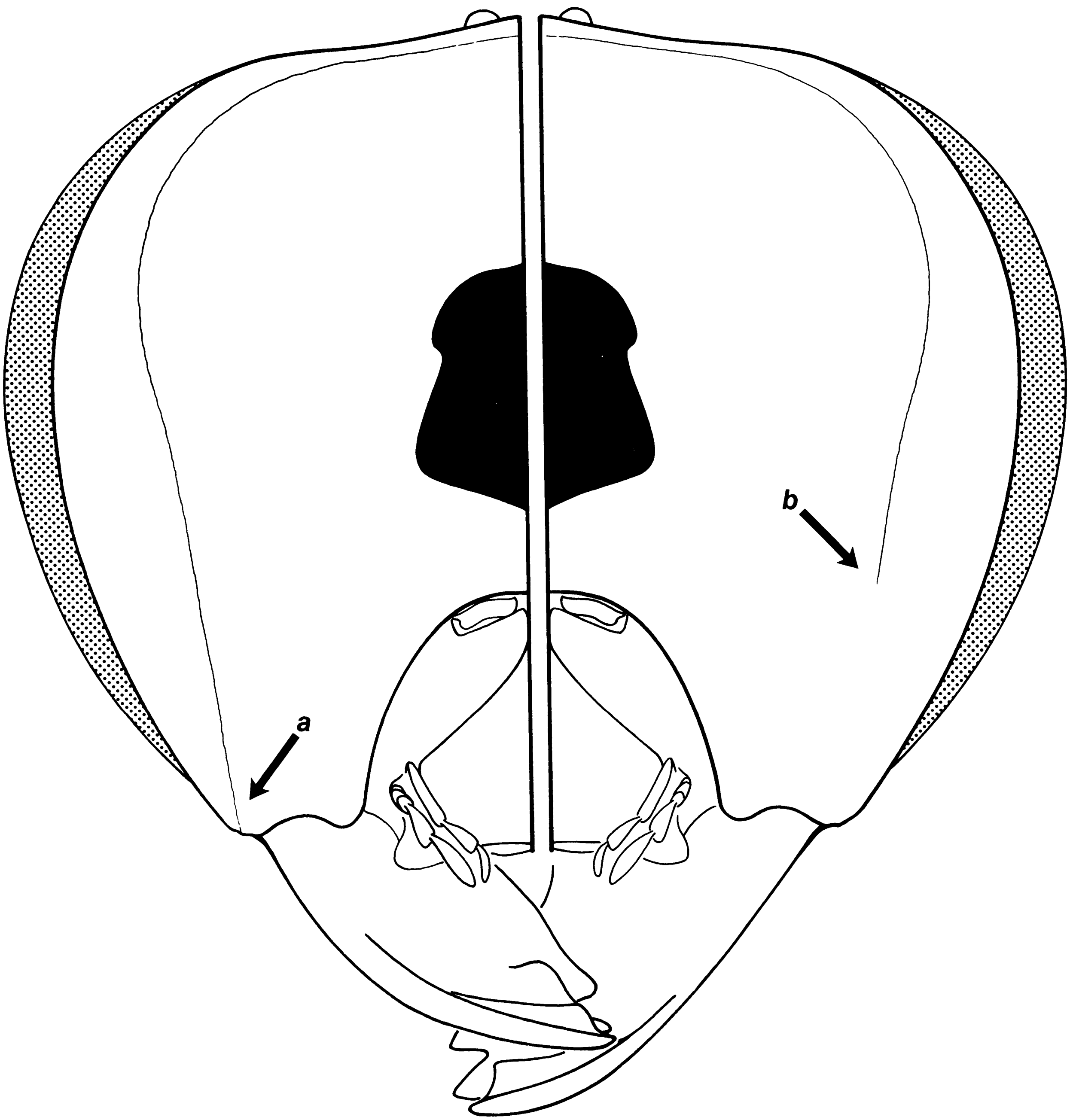


FIGURE 11 — *a*, Occipital carina extending to base of mandible (*Vespula vulgaris* group species); *b*, occipital carina ending above base of mandible (*Vespula rufa* group species).

formed a spongy fibrous mass rather than distinct sheets. The latter nest was 10.7 cm in diameter and had one worker comb and one reproductive comb. The number of combs was not given for the first nest. Both nests were small, the first contained the foundress queen, 55 workers, and a *D. arctica* (Rohwer) female; the second lacked a foundress queen and contained 41 workers, 11 new queens, and 26 males. Additional evidence used to support the contention that *D. saxonica* occurs in North America was based on morphological analyses of workers, queens, and males. One critical character used in identifying the species was based on the ratio between head-width and the length of the oculo-malar space. A second distinguishing feature was the sequence of tyloides on male antennae, while the last concerned the color patterns on abdominal terga II to V.

An examination of European literature on *D. saxonica* revealed a number of discrepencies with the above report. For example, the nest architecture reported by Kemper and Döhring (*1967*, fig. 31) does not show a tiered envelope, nor did Løken (*1965*) report this as a characteristic of *D. saxonica* nests. Løken (*1964*) also gave a different tyloide sequence for males, In addition, the gaster color pattern of *D. saxonica* illustrated by Kemper and Döhring (*1967*) is vastly different from that mentioned by Wagner (*1978*) or illustrated by Yamane (*1975*). Evidently, there are also problems or areas of confusion in Norway concerning the relationship between *D. saxonica* and the closely related *D. norwegica* (Fab.) as Løken (*1964*) concluded her discussion of *D. saxonica* with (we) "need more investigation to settle the status of this wasp."

We also measured a series of seven workers from a *D. norvegicoides* nest from Montana, which showed two of these workers had head-width to oculo-malar space ratios intermediate in value between *D. saxonica* and *D. norvegicoides* as given by Wagner (*1978*).

Therefore, before deciding on the validity of the occurrence of *D. saxonica* in North America, we would like to see more evidence comparing nest architecture, series of workers, males, and queens, and behavior of colony members of *D. saxonica* and *D. norvegicoides*.

D. saxonica is not included in the key.

Identification of Members of *Vespula* Species Groups

The species of *Vespula* are divided into the *V. vulgaris* species group (scavengers, often pestiferous) and the *V. rufa* (L.) species group (strictly predators on live prey, usually nonpestiferous). These groups are discussed more fully in the "biology" section. Although the separation between them is based on morphological features as well as biological ones, these characteristics are difficult to see and interpret. Since they are not essential for species identification, they have not been included in the key, and are given separately in this section.

Members of the *V. vulgaris* group have the occipital carina (a ridge on the rear of the head) well developed throughout its length and extending to the base of the mandibles (fig. 11 *a*). In addition, the first gastral tergum is not narrowed anteriorly and is not depressed. Its hairs are usually pale gray or yellow.

Members of the *V. rufa* group have the occipital carina prominent dorsally but ending well above the base of the mandibles (fig. 11 *b*). The first gastral tergum is narrowed anteriorly with a slight depression behind its anterior margin. The hairs on this tergum are black.

The occipital carina is almost completely concealed on intact specimens because of the dense hair on the head and the difficult viewing angle. It can be best seen (under magnification) by placing the severed head in clear fluid, such as alcohol or water.

Key to Vespinae in North America

Key to Genera

1. Vertex extending greatly above compound eyes; distance between lateral ocellus and occipital carina much greater than distance between lateral occelli (fig. 12*a*); one very large (≥20mm), brown and yellow species. .... genus Vespa L.

Vertex not or only slightly extending above compound eyes; distance between lateral ocellus and occipital carina about the same as distance between lateral ocelli (fig. 12*b*) 2

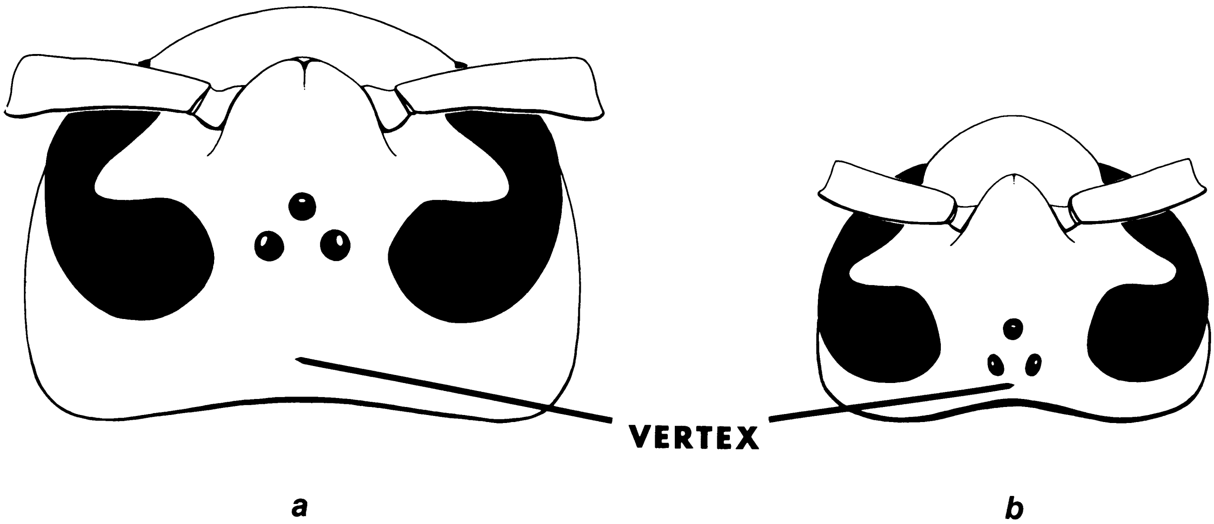


FIGURE 12.

2 Oculo-malar space narrow, compound eyes touching or nearly touching base of mandibles (fig. 13*a*) . . . . genus *Vespula* Thomson

Oculo-malar space broad, compound eyes remote from base of mandibles (fig. 13*b*) . . . . genus *Dolichovespula* Rohwer

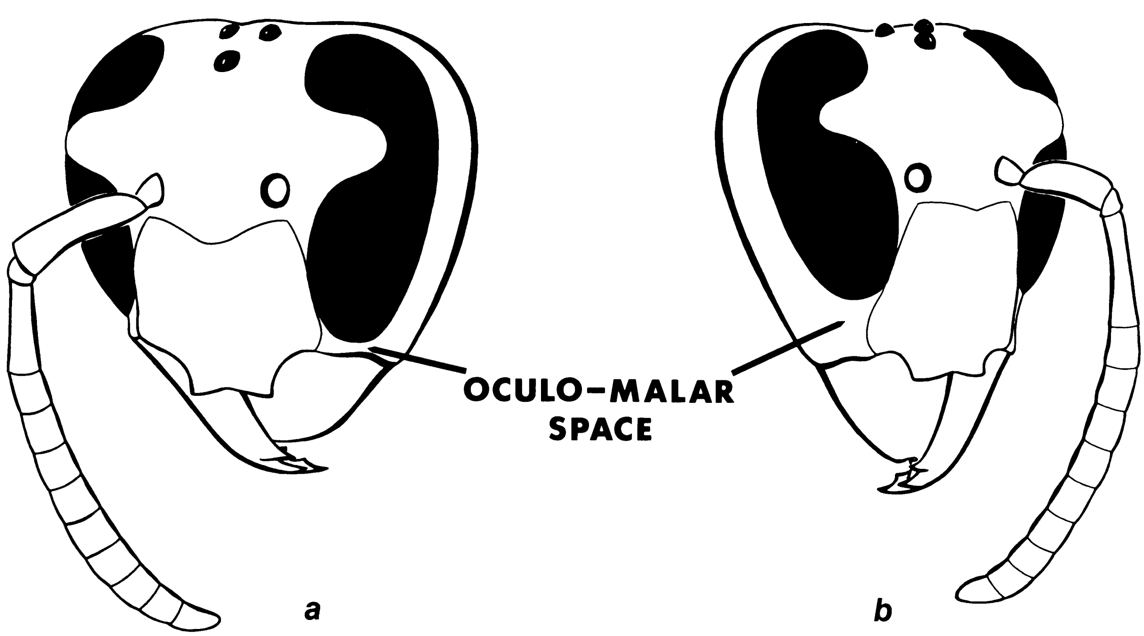


FIGURE 13.

Key to Species

Vespa

Gaster resembling figure 14. . . . . *V. crabro* L. (European hornet)

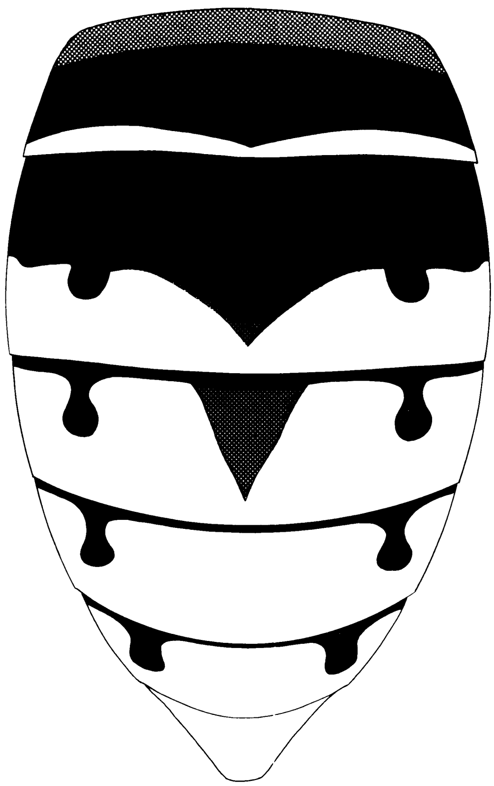


FIGURE 14.

Dolichovespula

1. Dorsal surface of first 3 terga entirely black (fig. 15*a*); large species (≥15mm) . . . . *D. maculata* (L.) (baldfaced hornet)

   First 3 terga with pale markings; smaller species (<15mm) 2

2. Pale markings white; usually with reddish spot on sides of tergum II (fig. 15*b*); rarely occurring south of Alaska and northern Canada . . . . *D. albida* (Sladen)

   Pale markings yellow 3

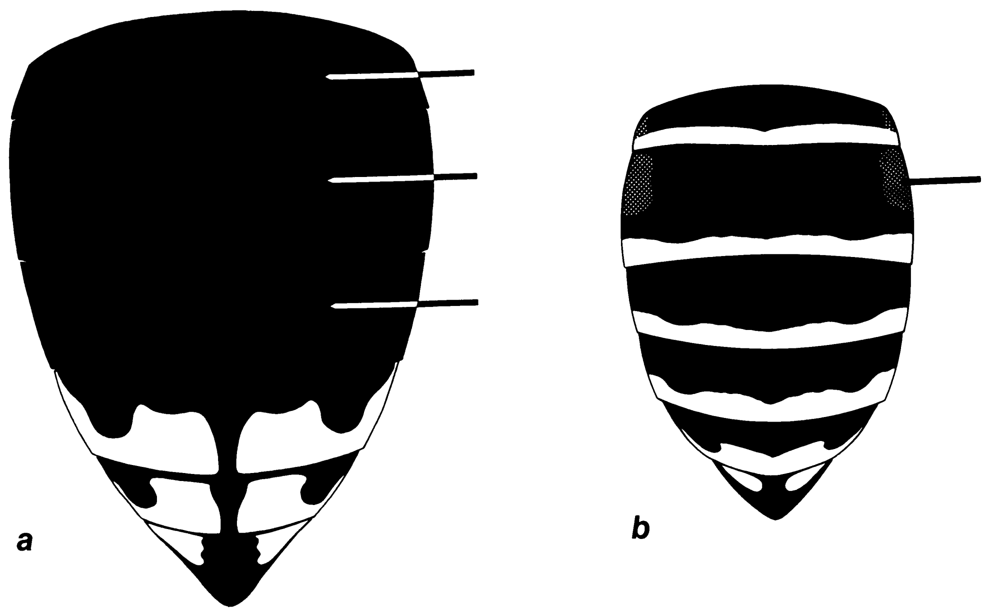


FIGURE 15.

3. Yellow genal band continuous (fig. 16*a*), though sometimes deeply notched; yellow of terga I and II sharply incised, usually interrupted medially (fig. 16*b*); common .... *D. arenaria* (Fab.) (aerial yellowjacket)

Yellow genal band usually widely interrupted (fig. 16*c*); yellow of terga I and II not sharply incised or interrupted medially (fig. 16*d*), but pattern sometimes closely approaches that of *D. arenaria;* not common .... *D. norvegicoides* (Sladen)

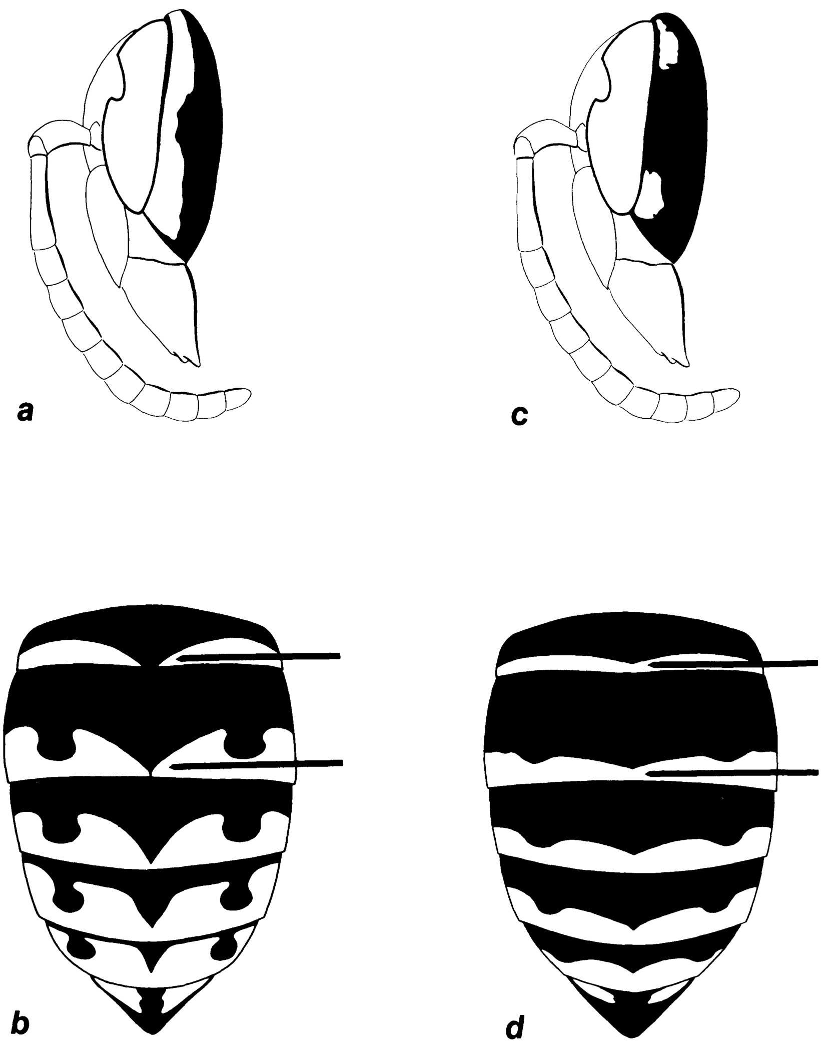


FIGURE 16.

Vespula

1. Pale marking white 2
   Pale markings yellow 3
2. Terga I and II with reddish markings (fig. 17*a*); rarely occurring outside Alaska and northern Canada . . . . *V. intermedia* (Buysson)
   Gaster without reddish markings; white band on posterior margin of tergum I usually interrupted medially (fig. 17*b*) . . . . *V. consobrina* (Saussure) (blackjacket)

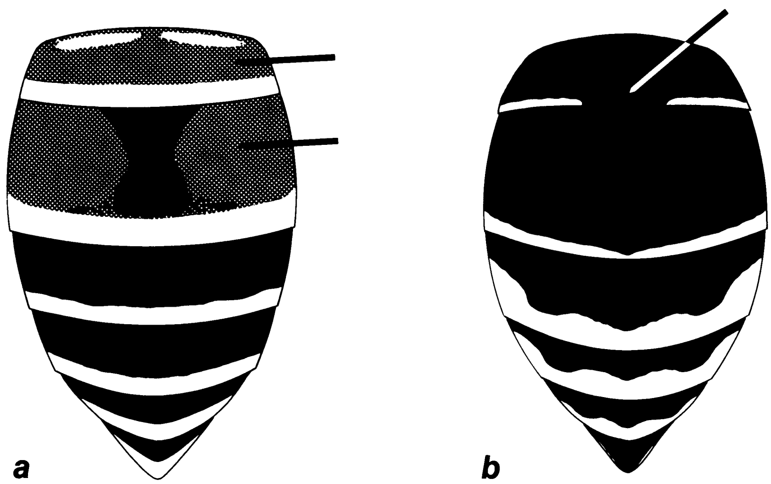


FIGURE 17.

3. Two yellow stripes on scutum (fig. 18*a*) 4
   Scutum without stripes (fig. 18*b*) 5

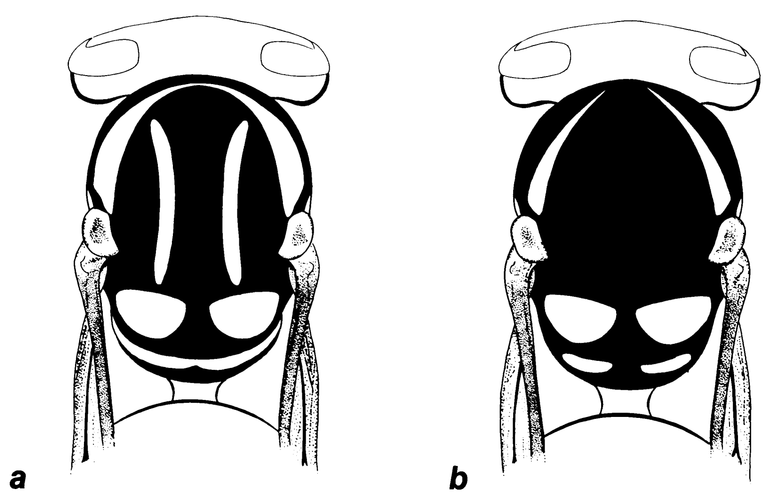


FIGURE 18.

4. Gaster resembling figure 19*a*; not occurring west of the Rocky Mountains . . . . *V. squamosa* (Drury) (southern yellowjacket)
Gaster resembling figure 19*b*; not occurring east of the Rocky Mountains . . . . *V. sulphurea* (Saussure) (California yellowjacket)

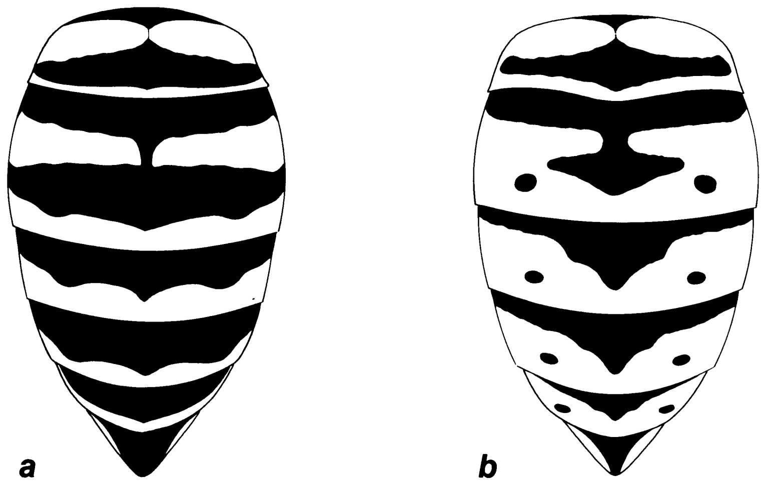


FIGURE 19.

5. Usually with a continuous yellow ring dorsally around each compound eye (fig. 20*a*); medial black mark on tergum I usually diamond shaped (fig. 20*b*) . . . . *V. pensylvanica* (Saussure) (western yellowjacket)
Head without a continuous yellow ring dorsally around each compound eye (fig. 20*c*) 6

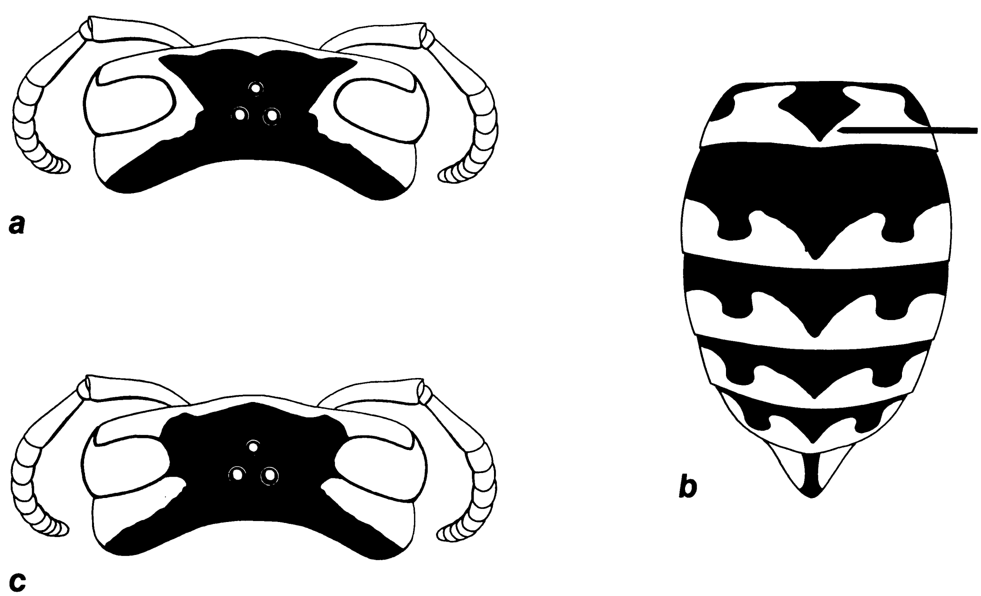
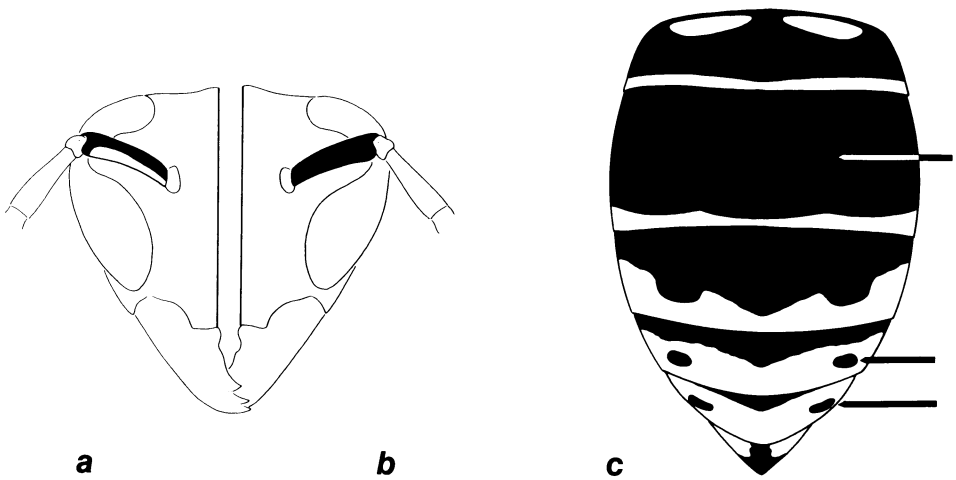


FIGURE 20.

6. First antennal segment yellow ventrally (fig. 21*a*) 7
First antennal segment without yellow, usually entirely black (fig. 21*b*), sometimes brownish distally 9

7. Gaster resembling figure 21*c*; extensive black region on tergum II never with 2 yellow spots; often with free, or nearly free, black spots on terga IV and/or V; not occurring west of the Rocky Mountains . . . . *V. vidua* (Saussure)
Gaster not as in figure 21*c* 8



a b c

FIGURE 21.

8. Gaster resembling figure 22*a*, the 2 yellow spots on tergum II often faint or absent, sometimes expanded (fig. 22*b*); medial margin of black region on tergum II broadly rounded; terga III, IV, and V usually without free black spots; yellow genal band usually interrupted (fig. 22*c*), rarely continuous . . . . *V. acadica* (Sladen)

Gaster resembling figure 22*e*, or with black regions expanded, varying to fig. 22*d*; when black regions expanded, medial margin of black region on tergum II tapering sharply; terga III, IV or V usually with some free, or nearly free, black spots; yellow genal band usually continuous (fig. 22*f*), sometimes with central black spot, rarely with narrow interruption; occurring principally west of the Rocky Mountains . . . . *V. atropilosa* (Sladen) (prairie yellowjacket)

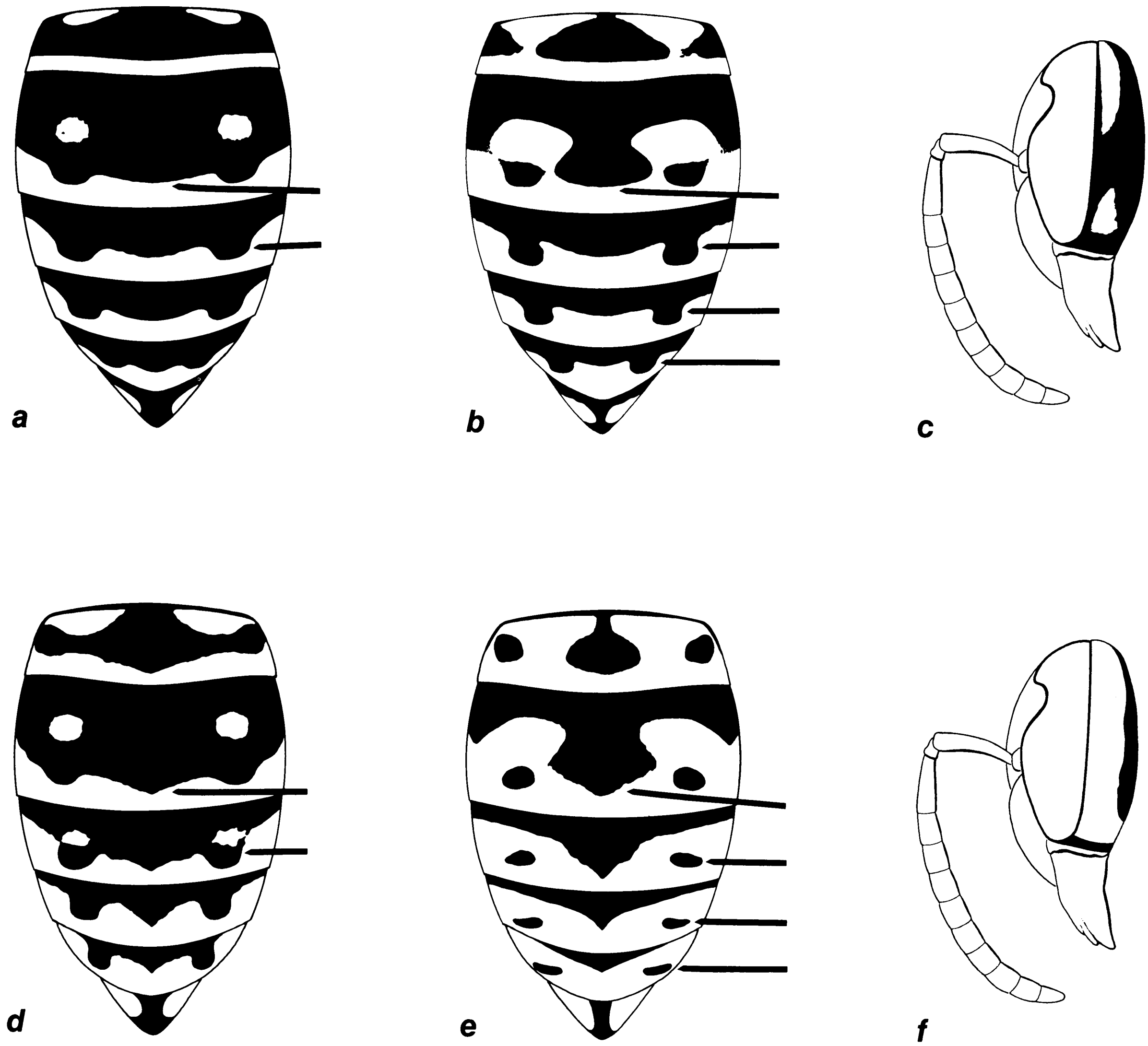


FIGURE 22.

9. Yellow genal band interrupted with black (fig. 23*b*), sometimes only slightly; gaster resembling figure 23*a*, tergum I varying as shown . . . . *V. vulgaris* (L.) (common yellowjacket)
Yellow genal band continuous (fig. 23*c*) 10

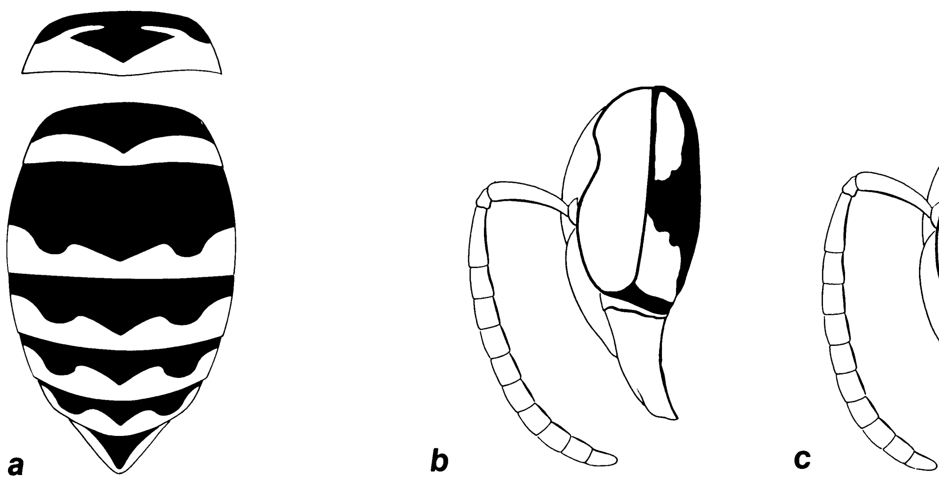


FIGURE 23.

10. Gaster usually resembling figure 24*a*, black regions sometimes expanded, varying to figure 24*b*; tergum II usually with free, or nearly free, black spots; medial black mark on tergum I usually diamond shaped . . . . *V. germanica* (Fab.) (German yellowjacket)
    Gaster resembling figures 24*c* or 24*d*; tergum II usually without 2 completely free black spots; not occurring west of the Rocky Mountains . . . .
11. Medial black mark on tergum I usually anchor-shaped (fig. 24*c*), although varying in width; common . . . . *V. maculifrons* (Buysson) (eastern yellowjacket)
    Medial black mark on tergum I usually V-shaped (fig. 24*d*), although varying in width; not common . . . . *V. flavopilosa* Jacobson (hybrid yellowjacket)

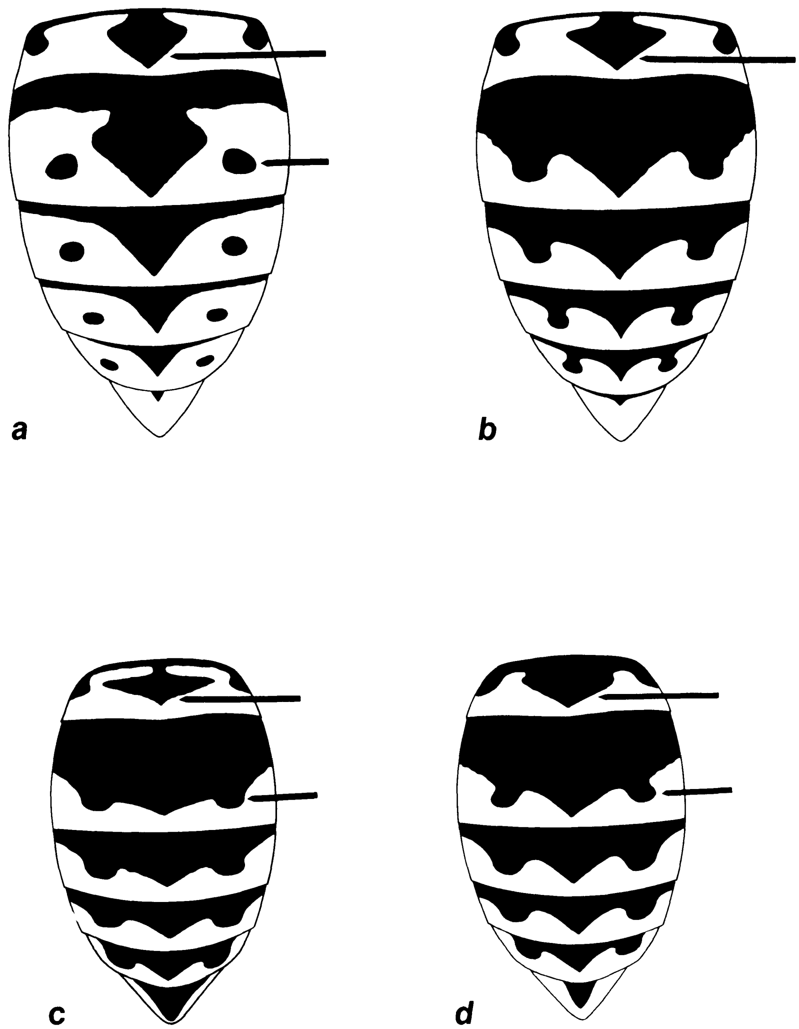


FIGURE 24.

Yellowjacket and Hornet Worker Gaster Patterns Drawn to Scale (fig. 25)

This section is intended as a quick reference guide to the gaster patterns of worker yellowjackets and hornets, and not as a substitute for the preceding key. Very few specimens will correspond exactly with the drawings, and extreme variant specimens may be encountered that will not be readily identifiable. The practice of collecting a series of specimens whenever possible will greatly facilitate identification of such individuals.

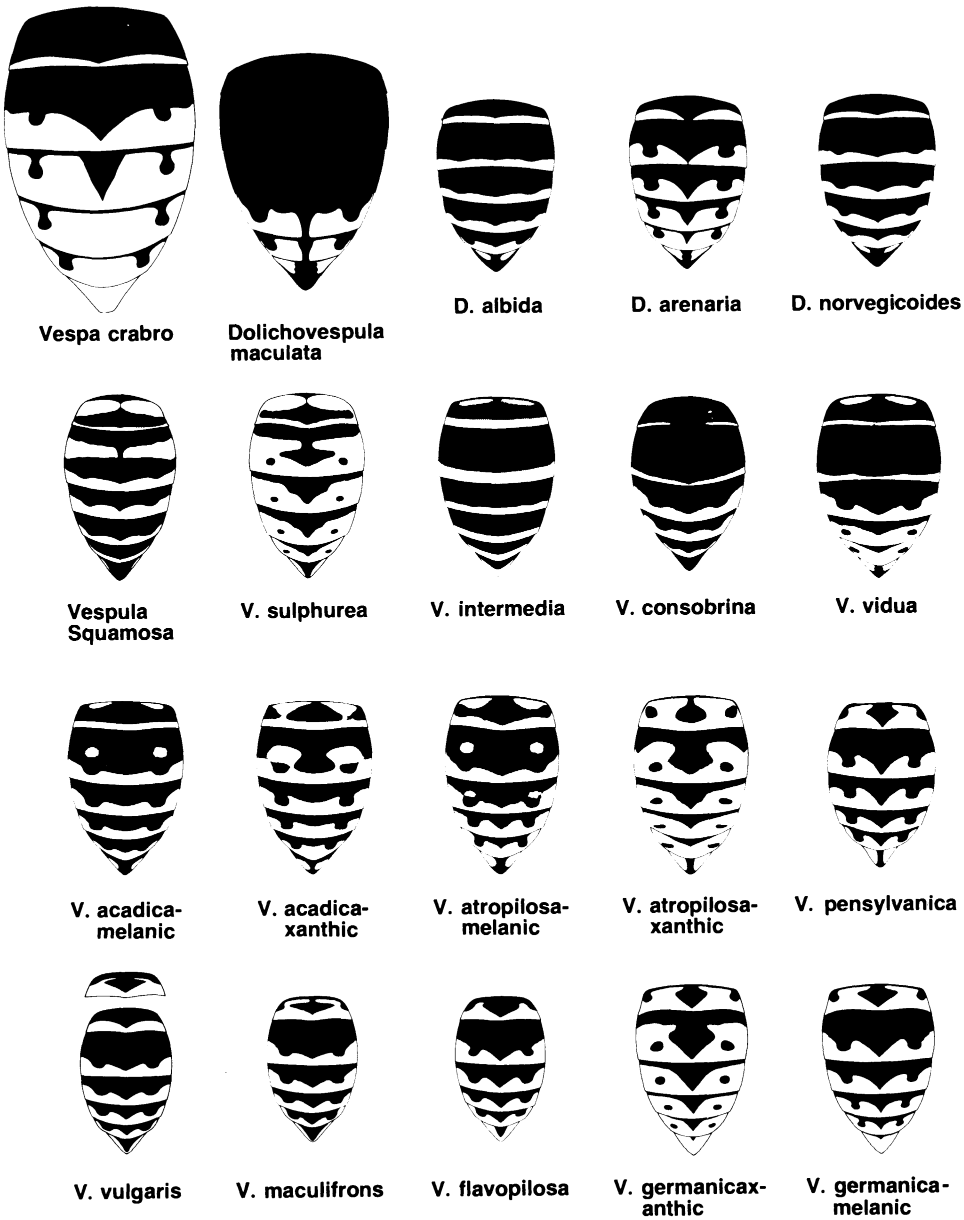


FIGURE 25 — Yellowjacket and hornet worker gaster patterns drawn to scale.

Vespa

V. crabro L. — Very large (≥20 mm); dark brown and deep yellow; anterior third of the first tergum reddish brown.

Dolichovespula

D. maculata (L.) — Large (≥15 mm); gaster mostly black; white markings on last 3 terga.

D. albida (Sladen) — Black and white; usually with lateral reddish spots on first 2 terga.

D. arenaria (Fab.) — Yellow of first terga sharply incised, usually interrupted medially.

D. norvegicoides (Sladen) — Yellow of first 2 terga continuous; yellow of most terga usually not as sharply incised as in *D. arenaria.*

Vespula

V. squamosa (Drury) — Distinctive pattern as illustrated; wide black "hourglass" marking on second tergum.

V. sulphurea (Saussure) — Distinctive pattern as illustrated; 2 yellow stripes on scutum distinguish *V. sulphurea* and *V. squamosa* from all other species.

V. intermedia (Buysson) — Black and white; large red areas on first 2 terga.

V. consobrina (Saussure) — Black and white; white band on posterior margin of first tergum usually interrupted medially.

V. vidua (Saussure) – Extensive black region on second tergum never with 2 yellow spots; usually with free or nearly free black spots on fourth and fifth terga.

V. acadica (Sladen)/*V. atropilosa* (Sladen) — Pattern of these 2 species highly variable; melanic form of *V. acadica* without 2 yellow spots on second tergum resembles *V. vidua*, but *V. acadica* almost never has free black spots on fourth and fifth terga; melanic form of *V. acadica* with 2 yellow spots resembles melanic *V. atropilosa*, but medial margin of black region on second tergum is broadly rounded in *V. acadica*, sharply tapering in *V. atropilosa*; xanthic forms of *V. acadica* and *V. atropilosa* resemble each other, but *V. atropilosa* usually has some free or nearly free black spots on third, fourth, and fifth terga.

V. pensylvanica (Saussure) — Diamond-shaped black mark on first tergum; similar to melanic *V. germanica*, but *V. pensylvanica* has continuous yellow ring dorsally around each compound eye.

V. vulgaris (L.) — Resembling *V. maculifrons* or *V. flavopilosa* when yellow on first tergum is expanded, but *V. vulgaris* has yellow genal band interrupted with black.

V. maculifrons (Buysson) — Distinctive anchor or arrow-shaped medial black mark on first tergum as illustrated.

V. flavopilosa Jacobson — Resembling *V. maculifrons*, but medial black mark on first tergum of most *V. flavopilosa* is V-shaped, without the very narrow "neck" of the mark on *V. maculifrons.* Highly xanthic *V. flavopilosa* may have 2 free black spots on second tergum, and therefore closely resemble *V. germanica.*

V. germanica (Fab.) — Diamond-shaped black mark on first tergum; usually with 2 free or nearly free black spots on second tergum. Highly melanic form is not common.

BIOLOGY

General

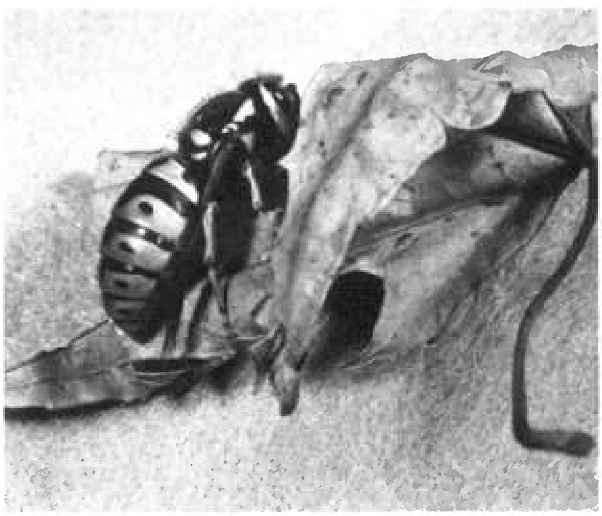
Vespidae (Stenogastrinae, Polistinae, Vespinae) are extremely diverse (Akre and Davis, *1978*). Behavior varies from presocial to eusocial. Most vespids build nests of masticated vegetable fiber initiated by a single queen (haplometrosis) or by a number of queens that cooperate (pleometrosis). Prey usually consists of live arthropods, although several members will scavenge flesh from dead animals.

All colonies of Vespinae (*Provespa, Vespa, Vespula, Dolichovespula*) are initiated by a single queen, and all build nests of paper carton. The nests consist of a number of rounded combs attached one below another. The combs are usually covered with a many-layered envelope. Some species primarily construct subterranean nests, some aerial nests, and others utilize either location. Colonies vary in size from less than a hundred individuals to several thousand. The Vespinae are the only wasps known to construct special cells on the combs to rear queens.

Since there is only a single species of *Vespa* (hornets) in North America, biological information is included with the species discussion.

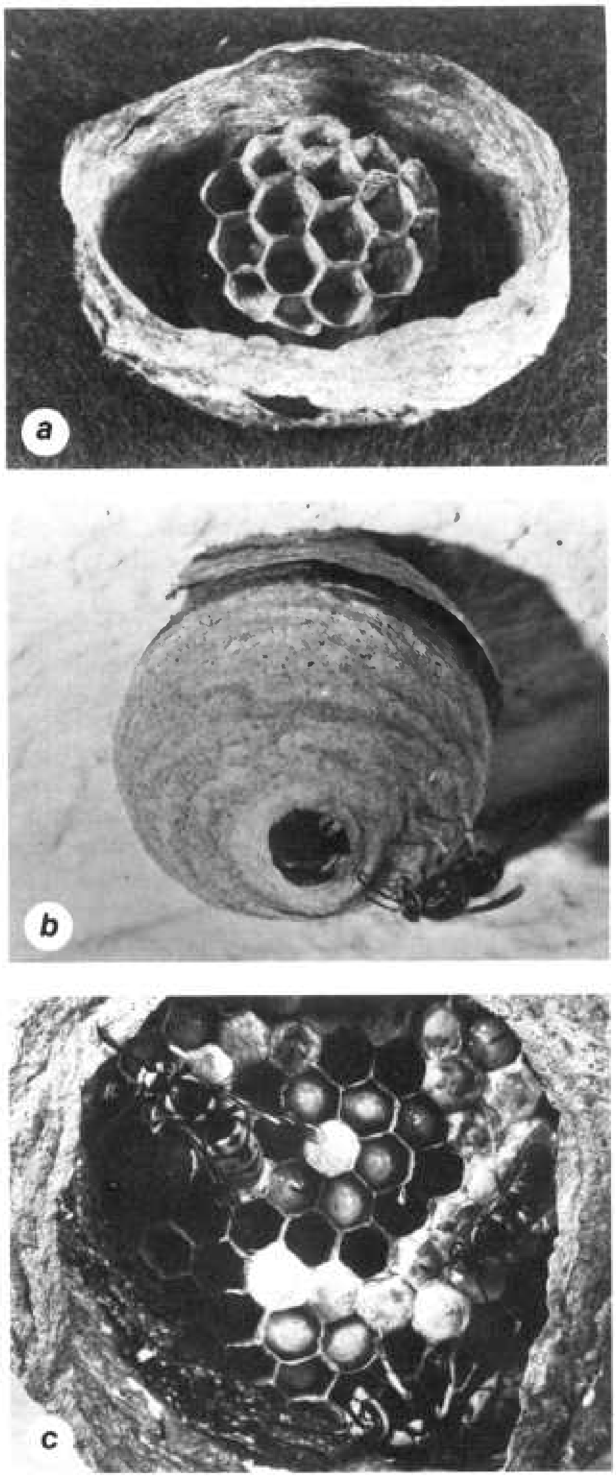
Newly produced yellowjacket (*Vespula*, *Dolichovespula*) queens are the only members of the colonies to survive the winter. These queens overwinter in sheltered locations, such as under loose tree bark or in decaying stumps, and emerge from hibernation during the first warm days of spring, usually in April or May (fig. 26). Soon after emerging, they begin to feed on flowers and other sources of nectar, and will also catch and malaxate arthropod prey. Ovaries of these queens are very small, but grow rapidly as reproductive diapause is broken. During this period, many queens are seen seeking nest sites, alighting under the eaves of houses, or entering cracks and crevices. After selecting a suitable location, the queen gathers plant fibers to construct the first cells of the nest. This fiber is usually gathered from weathered wood but may be collected from decayed wood or even living plants.

The queen nest (fig. 27) ultimately consists of



PN–6529

FIGURE 26 — *Vespula pensylvanica* queen in typical diapause position.



PN–6530

FIGURE 27 — *a*, Queen nest; *Vespula pensylvanica*; *b*, queen nest; *Dolichovespula arenaria*; *c*, nest of *V. atropilosa* with queen and first workers; queen on edge of comb in bottom of picture.

20 to 45 cells covered by a paper envelope. The queen lays eggs in the cells as they are constructed and forages for nectar and arthropod prey to feed the developing larvae. In about 30 days, the first 5 to 7 workers emerge and assume such duties as cell and envelope building, foraging for prey and nectar, and nest sanitatation (Akre et al., *1976*). After a short period of additional foraging, the queen no longer leaves the nest, and her primary function is to lay eggs. Workers are much smaller than the queen, and under normal colony conditions they do not lay eggs. Until this time, colony growth is slow but becomes exponential by midsummer as successive broods of workers emerge. The general, multitiered architecture of the vespine nest is apparent at this time with horizontally arranged combs comprised of ventrally open cells, typically enclosed in a paper envelope.

Later in the season, the workers start building the larger reproductive cells in which both males and queens are produced; males are also reared in worker cells. The colony enters a declining phase shortly thereafter when workers pull larvae from the comb and feed them to other larvae or discard them. During this period, in late summer or autumn, workers of several species are much more likely to sting, even when away from the nest. When new queens and males emerge, they leave the nest, mate (fig. 28), and the fertilized queens hibernate. Large numbers of males are often seen at this time swarming on hilltops or near shrubs and other vegetation. Mating may enhance successful overwintering, at least in *Vespula* (MacDonald et al., *1974*). The next spring the cycle is repeated (fig. 29). More detailed explanations of this cycle are found in Duncan (*1939*), MacDonald et al. (*1974*), and Spradbery (*1973a*).

Yellowjackets do not store honey as do the bees and some of the other vespids. They feed their larvae meat (arthropods, especially insects) and probably nectar and honeydew (a sugary material excreted by plant lice and certain other plant-feeding insects). The adults feed on juices while malaxating prey in the nest. They also eat nectar and larval secretions. The exchange of alimentary liquids among colony members (trophallaxis) is a prominent activity in the colony.

Yellowjackets prey on a wide variety of insects, spiders, other arthropods, and even mollusks to feed their larvae. All species of *Dolichovespula* will usually attack only live prey although there are a few records of workers scavenging from animal carcasses (Greene et al., *1976*). *Vespula* spp. are frequently divided into the *V. vulgaris* species group (genus *Paravespula* Blüthgen of European workers) and the *V. rufa* species group (genus *Vespula* of European workers) (tables 1, 2; fig. 30; Bequaert, *1931;* MacDonald et al., *1974* and *1976*). Members of the *V. rufa* group have a shorter colony duration and smaller colonies than members of the *V. vulgaris* group (fig. 31, table 3). More importantly, *V. rufa*

FIGURE 28 — Mating of *Vespula pensylvanica*; queen on left.

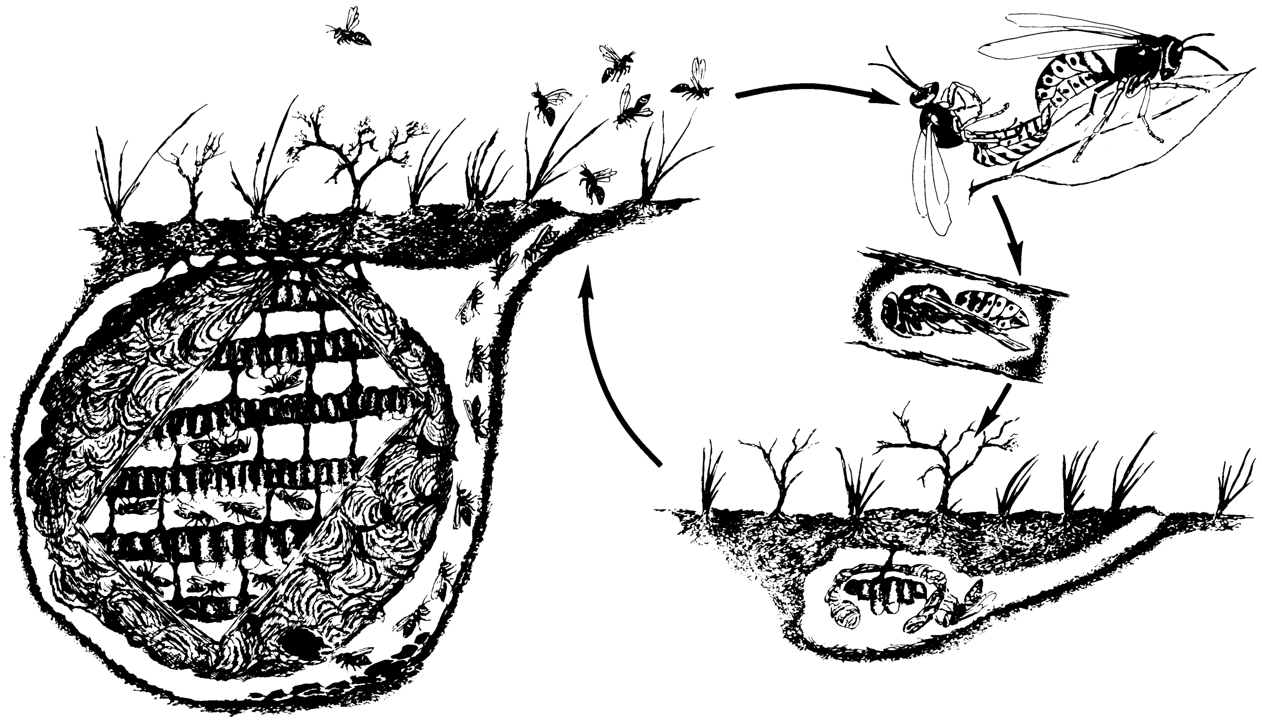


FIGURE 29 — Yellowjacket life cycle (*Vespula pensylvanica*): *a*, Mating; *b*, fertilized queen in diapause during winter months; *c*, queen nest beneath soil surface; *d*, nest at peak of colony development (J. Krispyn).

group species forage only for live prey, whereas members of the *V. vulgaris* group will also scavenge from animal carcasses, picnic tables, garbage cans, and many other locations, which makes them pestiferous to man (MacDonald et al., *1976*).

Vespula nests are usually subterranean, although some species will build their nests in hollow logs, trees, in attics, between walls, or on eaves of houses (Duncan, *1939*; Ebeling, *1975*; Green et al., *1970*; Kemper and Döhring, *1967*; Spradbery, *1973a*). Nest size varies from 300 to 120,000 cells, although most nests have 2,000 to 6,000 cells and are 8 to 15 cm in diameter. The largest nests are those of atypically perennial colonies, which do not die out over winter but continue on for an additional season with multiple queens. For example, the nest of one such *V. vulgaris* colony in California was nearly 4 ft long (Duncan, *1939*); a *V. squamosa* (Drury) nest in Florida was 9 ft tall (Tissot and Robinson, *1954*); however, the record for any vespine species clearly belongs to *V. germanica* in New Zealand, where perennial colonies are not uncommon (Thomas, *1960*). One nest was nearly 15 ft tall, probably contained several million cells in about 180 combs, and weighed an estimated 1,000 lb. Although the adult inhabitants of these nests must have numbered into the tens of thousands, counts were not made. For comparison, most nests of *V. vulgaris* group species contain 1,000 to 4,000 workers. *Dolichovespula* nests are usually aerial, although all species probably nest underground on occasion and at least two species (the Nearctic *D. arenaria* (Fab.) and the Palearctic *D. sylvestris* (Scopoli)) may do this frequently (Greene et al., *1976*; Archer, *1977a*; Spradbery, *1973a*). Most nests are small (300 to 1,500 cells), but those of vigorous *D. arenaria* colonies may contain up to 4,300 cells and those of *D. maculata* up to 3,500 cells.

A comparison of *D. arenaria* with *V. pensylvanica* (*V. vulgaris* species group) and *V. atropilosa* (*V. rufa* species group) is given in table 3. Although general comparisons cannot be made between *Vespula* and *Dolichovespula*, because the necessary information is not available, some of the characteristics compared in the table will probably hold true for many species. *D. arenaria* colonies (Greene et al., *1976*) and at least some European species of *Dolichovespula* (Spradbery, *1973a*) often build their nests on the eaves of houses or in other locations that bring them into contact with man, and, therefore, may sometimes be regarded as general nuisances; however, most *Dolichovespula* have small colonies, do not scavenge at picnic tables, and are not troublesome unless their nest is disturbed.

Members of the *V. rufa* group have small colonies of 75 to 400 workers, nests of 500 to 2,500 cells, and are strictly predaceous on live arthropods (table 1). Nearly all nests are subterranean or in decaying logs or stumps (MacDonald et al., *1974*, *1975a*). The nest of members of this group differs from that of the *V. vulgaris* group by having broad supporting buttresses, a strong flexible envelope paper, and a single comb of worker cells (table 2; MacDonald et al., *1974*; Spradbery, *1973a*). The nests of several species are also quite filthy and unkempt with remains of prey and dead workers incorporated into the envelope. Yellowjackets of the *V. rufa* group are usually considered highly beneficial because of their predation on a number of economically important insects (MacDonald et al., *1976*); however, even these

TABLE 1.—*Species groups, distribution, and colony characteristics of the subgenus* Vespula *(subterranean nesting yellowjackets) in North America. (Modified from MacDonald et al.,* 1976)

Species groups	Distribution	Colonies sampled	Group colony parameters	
Vespula vulgaris group				
vulgaris	Holarctic; transcontinental	[1]59	Size:	500 to 5,000 workers at peak.
maculifrons	Eastern	[2]78	Nest:	3,500 to 15,000 cells.
pensylvanica	Western	[3]62	Workers:	Predators plus scavengers.
germanica	Palearctic; now eastern North America	[1]30	Decline:	Late Sept. to Nov.-Dec.
flavopilosa	Eastern	[4]23		
Vespula rufa group				
acadica	Transcontinental	[5]4	Size:	75 to 400 workers at peak.
atropilosa	Western	[3,5]40	Nest:	500 to 2,500 cells.
consobrina	Transcontinental	[6]6	Workers:	Strictly predators.
vidua	Eastern	[6]10	Decline:	Late Aug. to early Sept.
intermedia	Transcontinental (Boreal)	0		
austriaca	Holarctic, transcontinental	0	(Unknown, social parasite of *V. acadica*)	
Uncertain affinities (currently placed with the *V. rufa* group)				
squamosa	Eastern, southeastern to Central America (social parasite of *V. maculifrons*)	[7,8]103	Size:	500 to 4,000 workers at peak.
			Nest:	2,500 to 10,000 cells.
			Workers:	Predators, reported to be scavengers.
			Decline:	Late Sept. to late Nov.
sulphurea	Western; southern Oregon, California into northern Mexico	0	Unreported; based on Duncan (*1939*) appears to exhibit a number of *V. vulgaris* group characteristics.	

[1]Spradbery, *1971.*
[2]MacDonald and Matthews, *198_a.*
[3]MacDonald et al., *1974.*
[4]MacDonald, Matthews, and Jacobson, *1978.*
[5]MacDonald et al., *1975a.*
[6]MacDonald and Matthews, *1976.*
[7]MacDonald and Matthews, *1975.*
[8]MacDonald and Matthews, *198_b.*

TABLE 2.—*Nest architectural characteristics of genus* Vespula—*subterranean nesting yellowjackets*

Species group	Nest architectural parameters
Vespula vulgaris group	Large nest—ultimately 3,500 to 15,000 cells. Several worker-cell combs. All suspensoria cordlike. Fragile envelope.[1] Scalloped envelope paper.
V. rufa group	Small nest—ultimately 500 to 2,500 cells. One worker—cell comb. Top suspensoria buttresslike. Pliable envelope. Laminar envelope paper.
V. squamosa	Large nest—ultimately 2,500 to 10,000 cells. Several worker-cell combs. All suspensoria cordlike. Pliable envelope. Laminar envelope paper.

[1]Envelope either gray (*V. pensylvanica, V. germanica*) or tan (*V. vulgaris, V. flavopilosa, V. maculifrons*).

yellowjackets are sometimes pestiferous to man as they frequently nest in manmade structures or in the yards of homes. In all cases, the wasps are a stinging hazard only after the colony is disturbed.

Members of the *V. vulgaris* group have larger colonies, larger nests, and a longer colony duration (table 1). These yellowjackets are frequently pestiferous. For example, *V. pensylvanica* commonly nests near well-watered yards in the dry areas of the Pacific Northwest, and numerous telephone calls were received from homeowners during 1974-77 in Pullman, Wash., for assistance in removing or killing colonies. Perhaps more importantly, workers of all species belonging to this group will scavenge for flesh and sweets, which brings them into frequent contact with humans. This is especially true with the tremendous increase in recreational developments such as parks, roadside rests, resorts, and in activities such as backyard cooking, hiking, and camping. Concentrated garbage and other meat sources in some of these areas have created a vast food supply for these scavenger species.

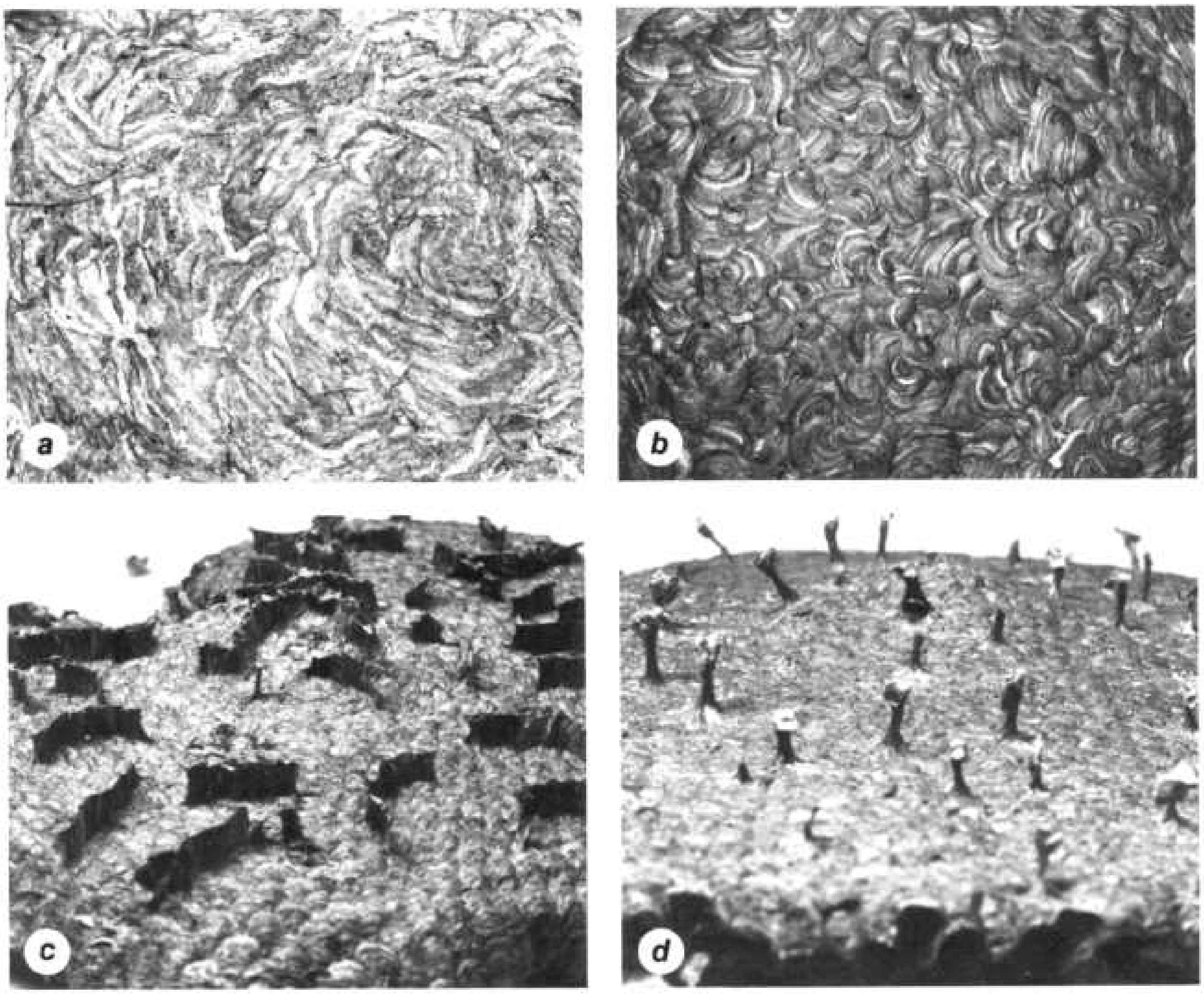
One of the notable aspects of late-season sampling of social wasp colonies is the variety and quantity of arthropods associated with the nest. Subterranean yellowjacket colonies, with large accumulations of wastes and bodies of dead individuals in the soil beneath the nest, support several species of associates, often in very large numbers. Expectedly, associated fauna in aerial nests is less varied and occurs in much smaller numbers. Spradbery (*1973a*) provided a general treatment of associates. This discussion concentrates on the most common and abundant associates found with Nearctic yellowjacket species. Colony associates can conveniently be separated into those actually invading the nest proper of active colonies and those developing in the soil beneath subterranean nests or invading abandoned (or nearly abandoned) nests.

Active yellowjacket and hornet colonies harbor very few nest invaders. The most important of these is an ichneumon wasp, *Sphecophaga vesparum burra* (Cresson). This pupal parasite (parasitoid) is a frequent occupant in nests of the *V. rufa* group, less common and less abundant in *Dolichovespula* nests, and rarely found in nests of the *V. vulgaris* group (with the exception of *V. vulgaris* nests, where it occurs frequently). Adverse effects on incipient *V. atropilosa* colonies may occur, but heavy parasitism is undocumented in other species. The only additional common nest invaders are cockroaches (*Parcoblatta* Hebard spp.), which occur in nests of *V. squamosa* in the southeast. These scavengers roam about the nest proper in over 70 percent of *V. squamosa* colonies but elicit no response from their hosts. Indeed, the cockroaches may assist in nest sanitation; a close relationship with the yellowjackets is suggested by the deposition of cockroach oothecae (egg cases) inside the layers of the nest envelope (MacDonald and Matthews, *198_b*). At least in the southeast, viable aerial colonies of *D. maculata* occasionally harbor cockroaches, but they are a different species of *Parcoblatta*.

In contrast to the paucity of nest-invading associates, numerous associates are found in the nest cavity of subterranean colonies and the decomposing carton of abandoned and nearly abandoned nests. Particularly productive is the waste-soaked soil beneath subterranean nests, which supports huge numbers of scavenger fly larvae. The most prevalent and abundant species is *Dendrophaonia querceti* (Bouche) (Diptera: Muscidae). Two other muscids, *Fannia canicularis* (L.) and *F. scalaris* (Fab.), are very common, although the rather cryptic larvae are more difficult to detect. Eggs of all three flies are laid on the outside of the nest envelope, from which the fly larvae drop into the soil beneath the nest. Occurring less frequently, but often in extremely large numbers inside a decomposing subterranean nest, are larvae of *Triphleba lugubris* (Meigen) (Diptera: Phoridae). Most likely scavengers on dead brood in the nest, *T. lugubris* invade cells containing developing (or possibly dying) queens; however, such invasion occurs in colonies in an advanced state of decline, and this species is not considered a significant mortality factor.

Appearance of scavenger associates is a late-season phenomenon associated with large nest size and an accumulation of wastes and other debris either inside the nest or in the soil beneath subterranean nests. In contrast, invaders of active colonies appear early in the colony cycle and may be present throughout the nesting season.

Among the vespine wasps are two obligate social parasites, *Dolichovespula arctica* and *Ves-*



PN–6531

FIGURE 30 — Comparison of paper and nest suspensoria of *Vespula atropilosa (V. rufa* group species) and *V. pensylvanica* (*V. vulgaris* group species). *V. atropilosa* has laminar paper (*a*) and mostly buttresslike suspensoria (*c*) *V. pensylvanica* has scalloped paper (*b*) and cordlike suspensoria (*d*).

TABLE 3.—*Comparison of nesting biology and behavior of 3 yellowjacket species. Data obtained from nests collected in several northwestern States and observations of captive colonies in Pullman, Wash.* (*Modified from Greene et al.,* 1976)

	Dolichovespula arenaria	*Vespula atropilosa*	*Vespula pensylvanica*
Approximate colony duration	3 to 4 months	3 to 4 months	4 to 5 months.
Nest sites	usually aerial, sometimes protected or subterranean	always protected, usually subterranean	always protected, usually subterranean.
Envelope composition	usually laminar	laminar	scalloped.
Queen nest pedical	often coated with glossy oral secretion	uncoated	uncoated.
Comb suspensoria	buttresslike	both types usually present	cordlike.
Number of worker combs	1 to 4; often multiple	1	1 to 6; usually multiple.
Reproductive cells on worker combs	often extensive on all worker combs	limited	limited except for final 1 or 2 worker combs.
Number of reproductive combs	0 to 4	0 to 3	0 to 3.
Reproductive production on reproductive combs	1 or 2 phases of largely homogeneous queen or male production	mixed queen and male production, no phases	largely homogeneous queen production.
Worker to reproductive cell ratios	0.3 to 1.9	0.5 to 2.6	1.5 to 34.9.
Oophagy by foundress queen	+[1]	–	–
Prey malaxation by foundress queen	continues for most of season	ceases early in season	ceases early in season.
Prey malaxation by new queens and males	+	–	–
Cap trimming by new queens	+	–	–
Mauling of new queens by workers	+	–	–
Gastral vibration by foundress queen and workers	+	+ (rare)	–
Nest sanitation	most waste removed	heavy waste accumulation	most waste removed.
Prey diversity	extensive, carrion usually not utilized	more limited, carrion not utilized	extensive, may utilize carrion heavily late in season.
Pronounced spraying of venom	+	–	–
Specophaga parasitism	usually light	usually heavy	rare.

[1]+, behavior or biology present; –, behavior or biology absent.

pula austriaca, which usurp colonies of other yellowjacket species. These yellowjackets lack a worker caste and are inquilines (permanent nest parasites), relying on the workers of the host to rear their brood. The hosts for *D. arctica* are two closely related yellowjackets, *D. arenaria* (Greene et al., *1976*) and *D. norvegicoides* (Sladen) (R.E. Wagner, Univ. Calif., Riverside; cited by Yamane, *1975*). The host of *V. austriaca* in North America was only recently discovered to be *Vespula acadica* (Reed et al., *1979*). Its Palearctic (European) host is *V. rufa* (Spradbery, *1973*a).

In addition to obligatory social parasitism, at least one species of yellowjacket is a facultative parasite. *Vespula squamosa*, a species that has workers, can establish colonies of its own, but frequently usurps colonies of *V. maculifrons* (MacDonald and Matthews, *1975*). There is also evidence of a *V. pensylvanica* usurping a nest of *V. vulgaris* (Akre et al., *1977*), intraspecific competition as evidenced by dead queens found in entrance tunnels (MacDonald et al., *1974*), and widespread interspecific and intraspecific competition in *V. maculifrons* colonies (MacDonald and Matthews, *198_a*). These data suggest that inter- and intraspecific usurpation in yellowjackets, rather than being uncommon, is widespread.

Predators of yellowjacket colonies are few; however, skunks dig up the nests of subterranean yellowjackets and eat the combs. For example, from 1974 to 1976 in the Pullman,

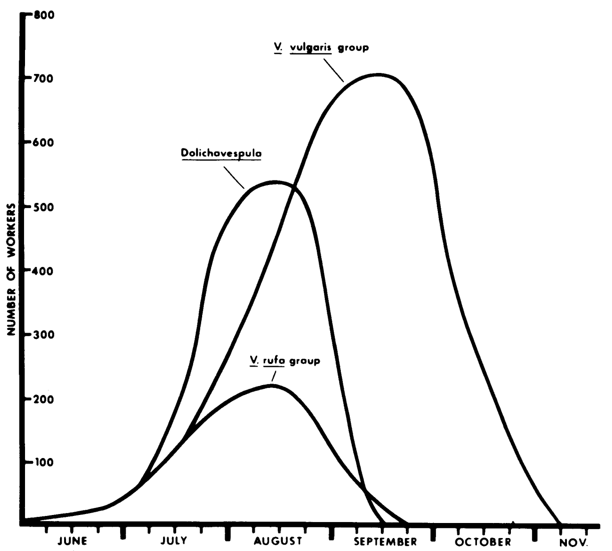


FIGURE 31—Schematic comparison of colony duration and size of *Vespula vulgaris* species group. *V. rufa* species group, and ***Dolichovespula*** ssp. based on number of workers at time of colony collection of *V. pensylvanica, V. atropilosa,* and *D. arenaria* in Pullman, Wash.

Wash., area, one to three nests (*V. atropilosa/V. pensylvanica*) were recorded as skunk victims each year. During 1977, 9 of 51 recorded *V. pensylvanica* colonies were lost to these predators. Other predators include coyotes (one *V. vulgaris* colony in the Blue Mountains of Washington, 1977) and bears (one *V. vulgaris* colony in mountains near La Grande, Oreg., 1975). In Georgia and Indiana, raccoons are one of the principal predators on colonies of *V. maculifrons, V. flavopilosa,* and *V. squamosa.* Other minor predators include birds, especially robins, which stand near the nest entrance where they catch and eat returning foragers. The impact of these predators on total yellowjacket populations is probably slight.

In the following sections, distribution data for the yellowjackets relies heavily on Miller (*1961*).

Hornets — *Vespa crabro*

Vespa crabro (European hornet) was introduced into the New York area between 1840 and 1860 (Shaw and Weidhaas, *1956*; van der Vecht, *1957*). Originally Palearctic, its estimated distribution in North America is given in figure 32. On the basis of isolated reports, *V. crabro* now occurs along the eastern seaboard from New England south into northern Georgia and Alabama, and westward to the Mississippi River from Tennessee north into the Ohio Valley. Scattered northern populations probably exist from the Dakotas to southern Ontario and Quebec, and the wasp has been reported as far south as New Orleans.

Few biological studies have been made of this species since the works of Janet (*1895, 1903*); however, the distribution of *V. crabro* in Europe was given by Guiglia (*1972*), and some behavioral aspects of one subspecies were recently investigated in Japan by Matsuura (*1969, 1970, 1971, 1973, 1974*). Little information is available on this species in America, and much of the information presented here is taken from Spradbery (*1973a*).

In Europe, *V. crabro* typically builds its nests in hollow trees. Nests are also found in thatched roofs, barns, attics, hollow walls of houses, and abandoned beehives. Similar nest sites are used in North America (fig. 33), and Duncan (*1939*) even reported some subterranean nests.

Nests built in unprotected locations are covered with a thick, brown envelope composed chiefly of coarse, decayed wood fibers, and, therefore, very fragile. Brown envelope and carton distinguish the nests of *V. crabro* from the more common gray nests of *D. maculata.* The envelope of *V. crabro* nests is usually composed of elongated shells or tunnels, which are distinct from the scalloped tan envelopes of *Vespula vulgaris* or *V. maculifrons.* In addition, cell size of *Vespa* is several times larger. Nests in protected locations, such as hollow trees or between walls of houses, typically have only a rudimentary envelope at the top of the nest, with most of the combs exposed.

V. crabro nests are often large because of the large individual cells, but contain relatively few cells. A typical mature colony has a nest of 1,500 to 3,000 cells in six to nine combs; the lower two to four combs contain queen cells. A huge nest collected in northern Georgia had 33 combs (nearly one-third reproductive), containing 5,566 cells (fig. 33 *j*). *V. crabro* colonies have a long seasonal cycle with eclosion of reproductives occurring from late August to November in eastern seaboard States. At its peak of development, a large colony consists of about 1,000 workers. Typical colonies, however, are more likely to have 200 to 400 workers at their peak.

Workers of *V. crabro* are predacious on a variety of insects, capturing large species such as grasshoppers and other orthopterans, flies, honey bees, and yellowjackets. Since they are powerful, agile wasps, they probably forage farther for prey than the smaller yellowjackets. The queen of *V. crabro* is attended by a "royal court" of workers, which are highly attracted to her (Matsuura, *1968*, *1974*). Workers fly at night, and are attracted to lighted windows in homes. "Sometimes ten or more will beat themselves against a window causing people inside to panic thinking they are trying to break the glass and invade the house to attack them. The very loud buzzing and the force with which they 'attack' the window is impressive" (C.W. Rettenmeyer, Univ. Conn., personal commun.). In the autumn,

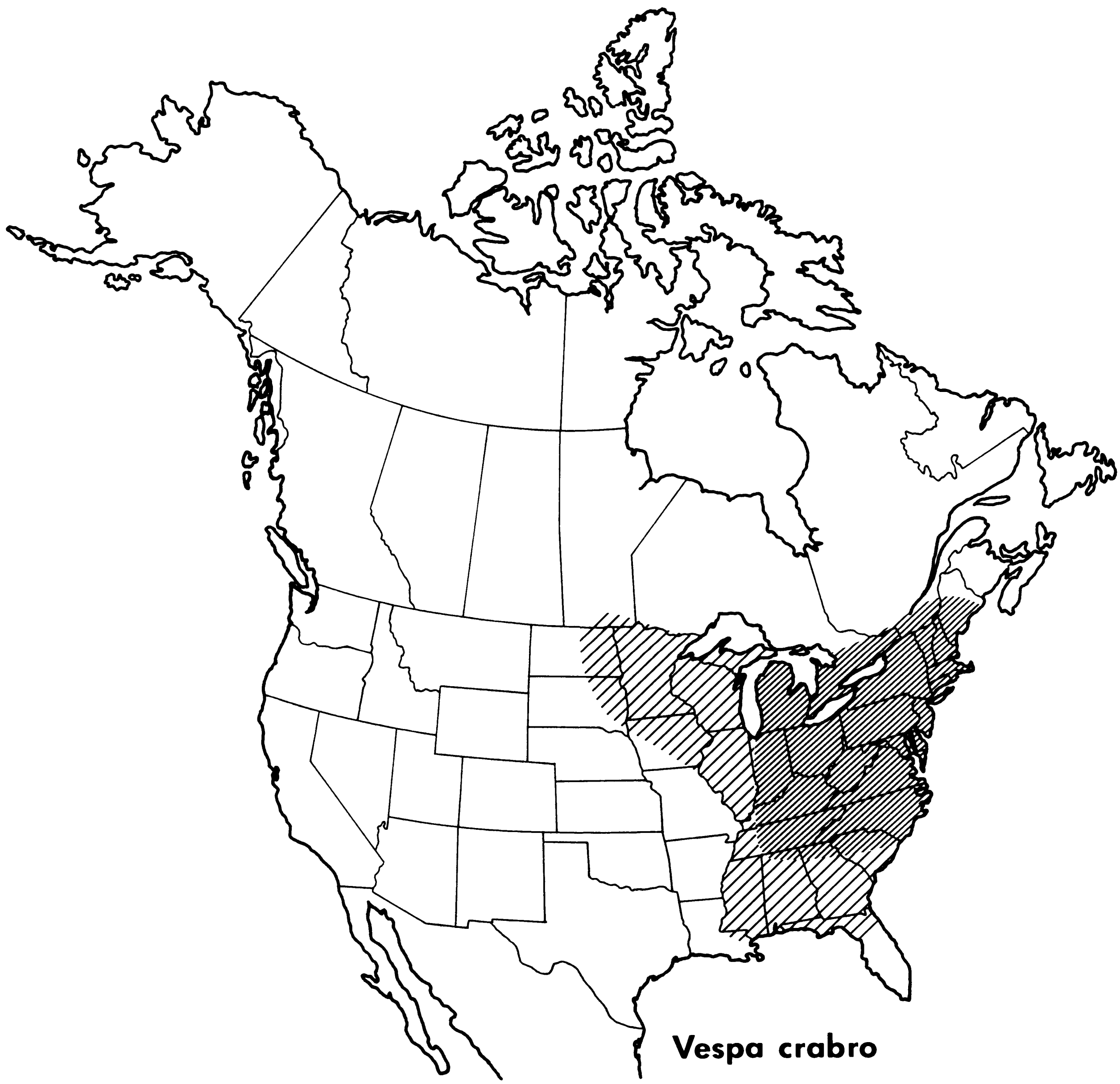
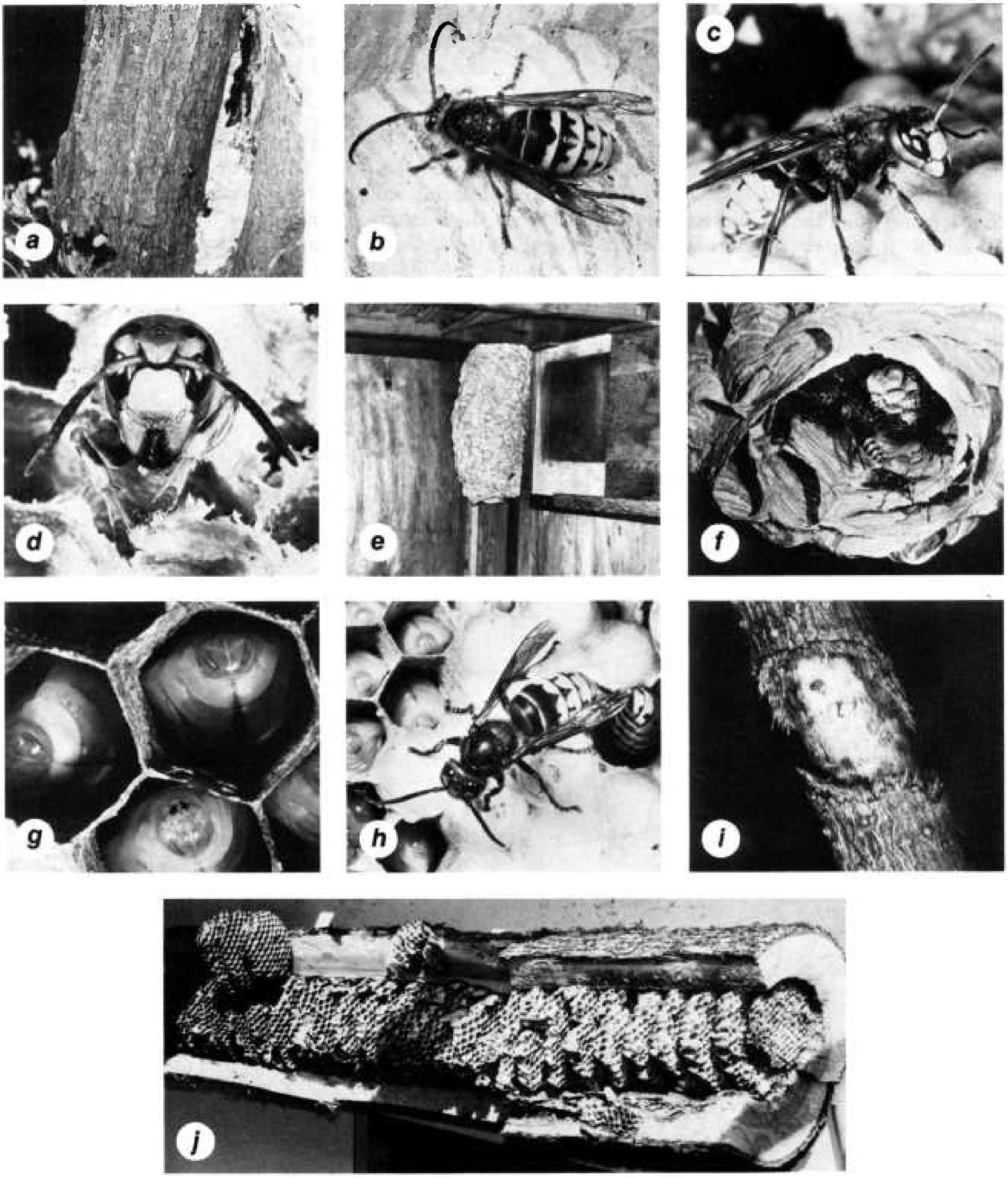


FIGURE 32 — Distribution of *Vespa crabro*. Lighter pattern indicates scattered occurrence.



PN-6532

FIGURE 33 —*Vespa crabro*: *a*, Typical nest site in hollow tree; *b*, male; *c*, queen on cell caps; *d*, fall queen emerging from pupal case; *e*, nest in playhouse; *f*, bottom of same nest; *g*, mature larvae; *h*, worker on comb; *i*, girdling of lilac (*a–i*, C.W. Rettenmeyer in Connecticut); and *j*, nest with 33 combs in sweet gum tree near Tate, Pickens County, Ga. (R.W. Matthews).

V. crabro males are often attracted to lights as well; therefore, in addition to morphological differences, a number of behavioral differences exist between this true hornet and yellowjackets.

Workers of *V. crabro* have been reported to girdle twigs and branches of numerous trees and shrubs, including lilac, birch, ash, horsechestnut, dogwood, dahlia, rhododendron, and boxwood (Hitchcock, *1970*; Shaw and Weidhaas, *1956*). Much of this girdling is probably done for sap and not for fiber collection as the workers are highly attracted to the girdled area, imbibe sap constantly, but usually do not carry fibers away. The plants are sometimes killed. This species is a pest of honey bees in apiaries in Japan and Europe (Matsuura and Sakagami, *1973;* Spradbery, *1973a*), but there are no reports of similar depredations to honey bees in America. *V. crabro* is primarily a forest species having few contacts with man and presenting a minimal stinging hazard.

Yellowjackets

Genus *Dolichovespula*

The five species of *Dolichovespula* occurring in the Nearctic Region are *D. albida* (Sladen), *D. arctica*, *D. arenaria*, *D. maculata*, and *D. norvegicoides*. Although this group has not been well studied, available data indicate there are sufficient morphological, physiological, and behavioral differences between *Dolichovespula* spp. and other yellowjackets to warrant their generic separation. Some of the more prominent morphological differences include adult and larval head structure, male genitalia, structures on the male antennae, and abdominal ganglia (Duncan, *1939*; Greene et al., *1976*). Although the strong attraction of certain *Vespula* spp. to the synthetic compounds 2,4-hexadienyl butyrate (Fluno, *1973*) and heptyl butyrate makes these chemicals a valuable sampling method for them, no attraction has been observed for any *Dolichovespula* spp. The venom chemistry of at least *D. arenaria* differs from that of *Vespula* spp. (O'Connor and Erickson, *1965*; A. Benton, Penn. State Univ., personal commun.). Most importantly, observations of *D. arenaria* behavior (Greene et al., *1976*) indicate this species has a noticeably weaker dichotomy between queen and worker castes than in observed *Vespula* spp., as well as a different pattern of reproductive production. A comparison of several behavioral aspects of *D. arenaria* and two *Vespula* spp. is given in table 3. Preliminary observations of *D. maculata* reveal this species also differs greatly from *Vespula*.

Dolichovespula nests are usually aerial, although all species probably nest underground on occasion and subterranean nests of *D. arenaria* are not uncommon in some areas. Typical nests are relatively small (300 to 1,500 cells), although exceptionally vigorous *D. arenaria* colonies may construct over 4,300 cells, and the largest *D. maculata* nests have approximately 3,500 cells. Mature nests are usually comprised of two to six combs. Envelope paper covering the nest usually consists of distinct laminar sheets, although there may be a high degree of scalloping and cellular construction in mature *D. maculata* nests. The paper itself is much stronger, more flexible, and more resistant to water damage than the comparatively brittle paper constructed by *Vespula* spp. Peak worker populations usually range from 200 to 700 individuals.

Dolichovespula are not attracted to protein baits and usually forage only for live prey, but occasionally will scavenge flesh from animal carcasses (Greene et al., *1976*). In this respect, their behavior seems "intermediate" between the *Vespula rufa* group species (strictly live prey) and the *Vespula vulgaris* group (frequent scavengers).

Dolichovespula albida

Dolichovespula albida is restricted almost entirely to the Hudsonian Zone of the North American Boreal Region (fig. 34). Miller (*1958, 1961*) considered this a valid species rather than a subspecies of the closely related *D. norvegicoides* since it retains its identity over its range even in areas in which it is sympatric with *D. norvegicoides*. Practically nothing is known of the biology and behavior of this species. Bequaert (*1931*) discussed two reports of subterranean and partially subterranean nests; one was 5 inches in diameter.

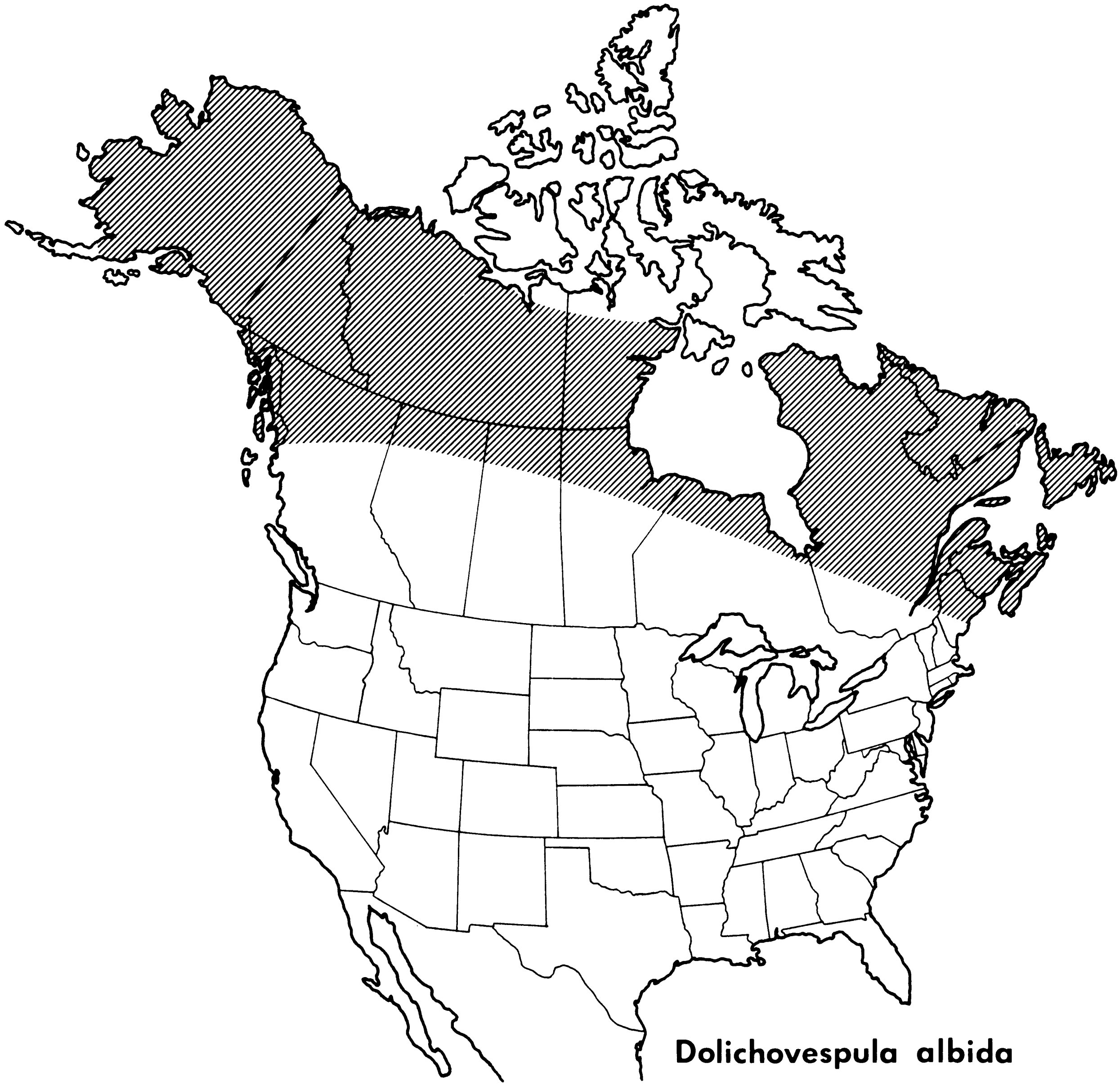


FIGURE 34 — Distribution of *Dolichovespula albida*.

Dolichovespula arctica

Dolichovespula arctica is distributed throughout the Boreal Region of North America, occurring from Alaska to Arizona and across to the eastern seaboard (fig. 35). Investigations of its biology have been limited (Taylor, *1939*; Wheeler and Taylor, *1921*), although recent studies have begun to reveal more about its complex behavior (Evans, *1975*; Greene et al., *1978*; Jeanne, *1977*).

D. arctica is an obligatory social parasite in colonies of *D. arenaria* (Greene et al., *1976*) and *D. norvegicoides* (R.E. Wagner, Univ. Calif., Riverside; cited by Yamane, *1975*), relying on host workers to raise its own offspring. A *D. arctica* queen invades a host nest early in the season before workers have emerged (Evans, *1975*). Although it may be attacked vigorously by the foundress queen at first (fig. 36*d*), the parasite becomes established as a nestmate within a day (Greene et al., *1978*; Jeanne, *1977*). The *D. arctica* queen may be highly aggressive and dominant in most interactions with its hosts, yet it feeds host larvae as well as its own and even participates in limited cell construction.

The parasite queen kills the host queen before much of her worker production is completed, shortening the lifespan of the colony and reducing the size of the mature nest relative to that of unparasitized colonies. It is still unknown how the *D. arctica*'s occupation of a colony usually terminates. In one chronologued colony, antagonism between parasite and host workers gradually increased after the queen's death, culminating in the slaughter of many workers by the larger, better-armored parasite; however, it is likely that this *D. arctica* was finally killed by the workers (Greene et al., *1978*). Although a host colony produces no new queens, the *D.*

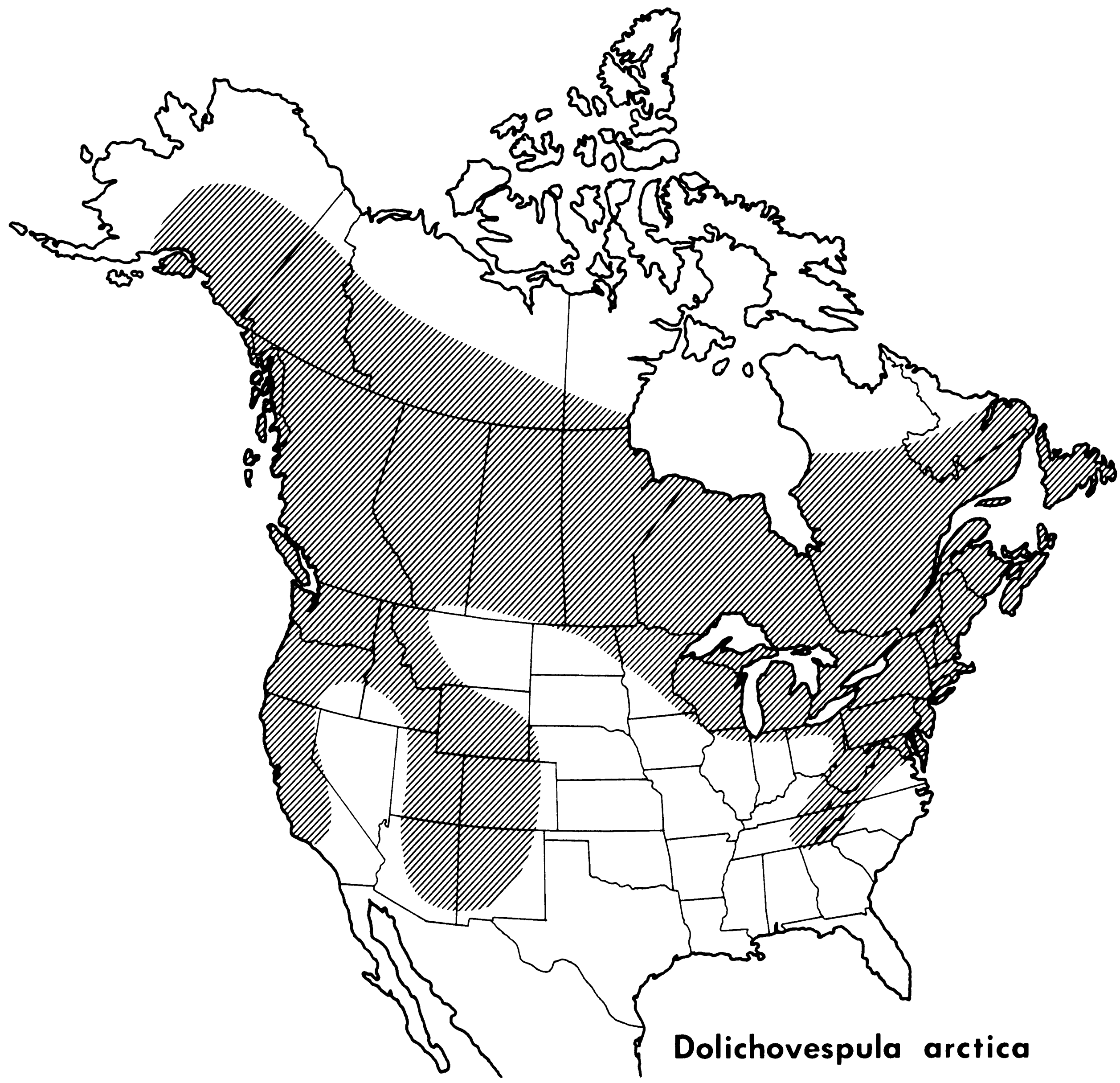
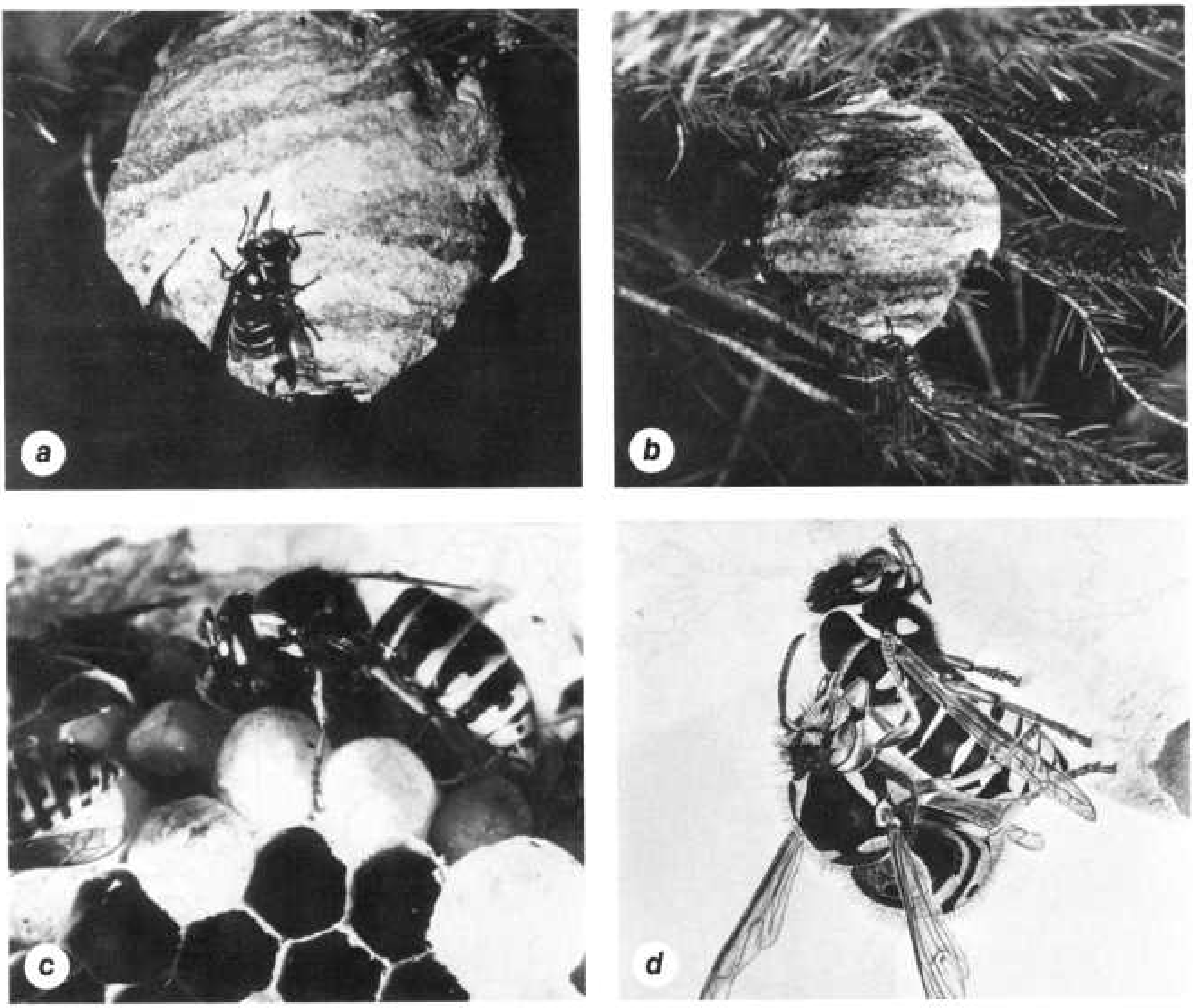


FIGURE 35 — Distribution of *Dolichovespula arctica*.



PN-6533

FIGURE 36 — *Dolichovespula arctica*: *a*, *D. arctica* queen on outside of *D. arenaria* nest (S.C. White); *b*, same nest, *D. arenaria* queen entering (C.F. Roush); *c*, *D. arctica* queen on comb of *D. arenaria* nest; and *d*, *D. arenaria* queen attacking *D. arctica*, which assumes a submissive posture.

arctica apparently cannot prevent the host workers' ovaries from developing, and some may start ovipositing during the final days of the parasite's occupation. Additional large numbers of unfertilized eggs may be oviposited by workers following the parasite's death, and a sufficient degree of colony cohesion may be maintained in some cases to rear a substantial brood of host male offspring to adulthood (Greene et al., *1976; 1978*).

Dolichovespula arenaria

Dolichovespula arenaria (the aerial yellowjacket) is transcontinentally distributed in the Boreal Region of North America, occurring from north-central Alaska to as far south as Arizona and New Mexico (fig. 37). It is "one of the commonest wasps in North America" (Miller, *1961*) and one of the most widely distributed. Although there are numerous papers on various aspects of its behavior and nest architecture, the only comprehensive study of its social biology is that of Greene et al. (*1976*).

D. arenaria nest construction begins as early as March in California, with many colonies declining in mid-June and totally dying out by July (Duncan, *1939*). In the mid-Atlantic States, colonies may be mature and producing reproductives by late June. In Washington, queens become active in April and nests are initiated from May to early June, with colonies entering decline in August. A few may endure throughout September. Nests are usually aerial and are constructed from a few centimeters above ground in grass, shrubs, and bushes to the very tops of trees (fig. 38). They are also commonly found on houses and in sheds, garages, and many similar manmade structures. Colonies may sometimes be situated beneath rocks or even below ground, with workers excavating soil to allow for nest expansion as in *Vespula* spp. (Greene et al., *1976*). During the summer of 1977, 14 subterranean nests with excavating workers were located in the mountains near La Grande, Oreg., and near

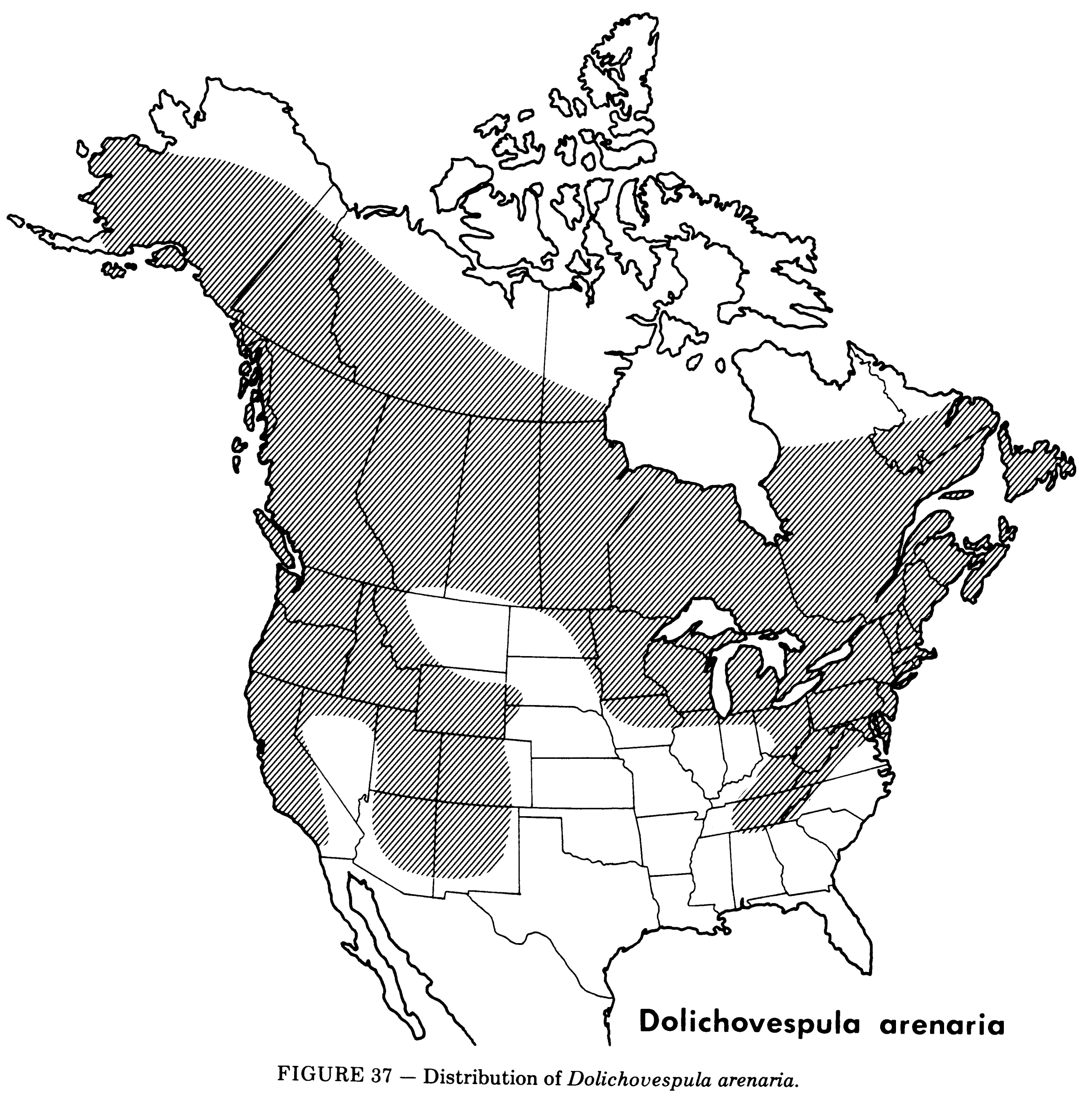
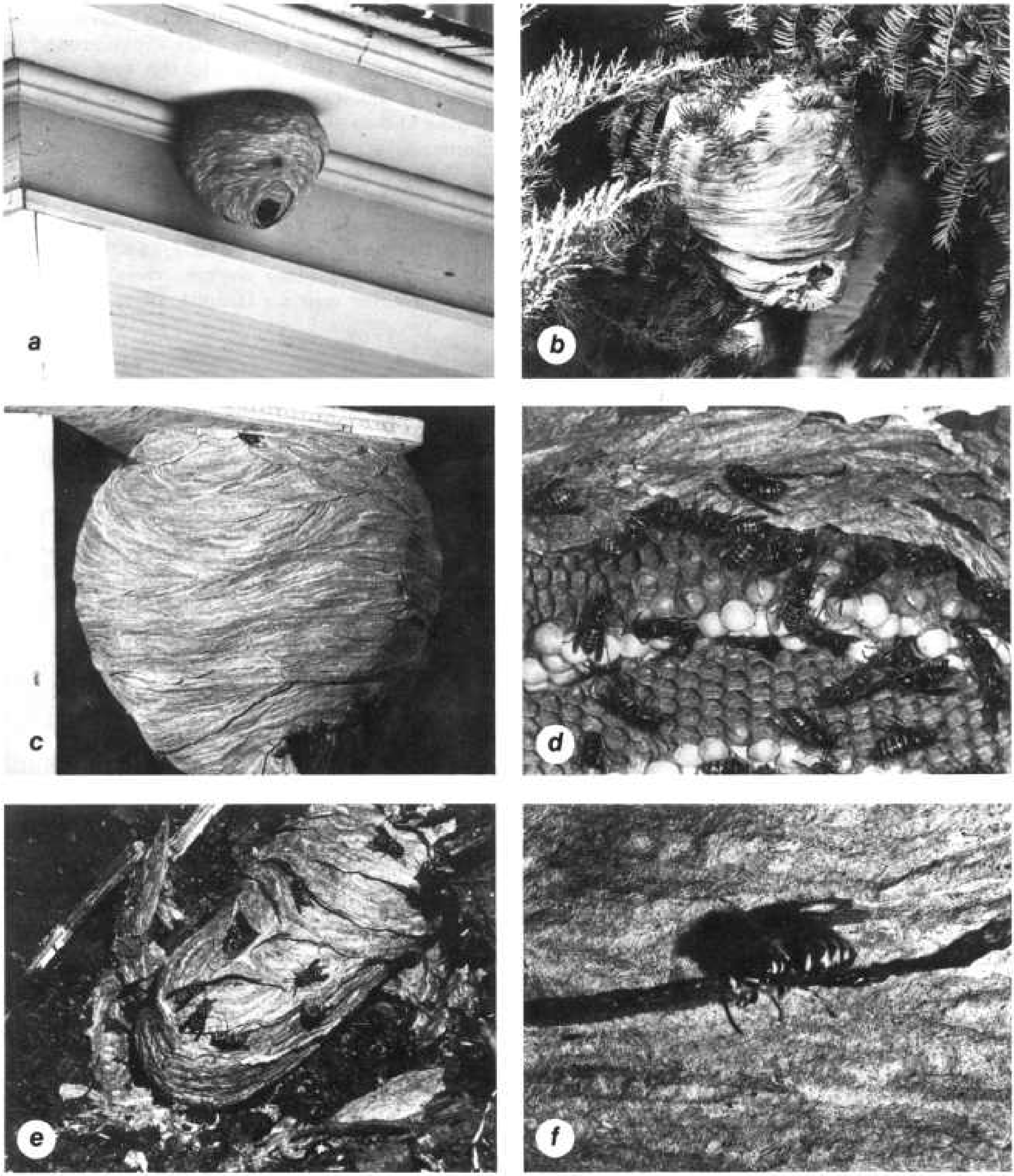


FIGURE 37 — Distribution of *Dolichovespula arenaria*.



PN-6534

FIGURE 38 — *Dolichovespula arenaria*: *a*, Typical nest site on eave of house, Elberton, Wash; *b*, typical nest site in evergreens about 38 cm above soil, Pullman, Wash.; *c*, nest taken from eave of house, glued to a board, and transplanted in another location; *d*, envelope removed from same nest showing combs and workers; *e*, subterranean nest in mountains near La Grande, Oreg. (C.F. Roush); *f*, worker placing fiber (seen as dark band) on nest envelope.

Harrison, Idaho, suggesting that such nests may not be uncommon in similar habitats throughout western North America.

Colony size of *D. arenaria* may vary greatly from year to year. For example, most nests constructed by colonies in southeastern Washington in 1974 were small, with diameters rarely exceeding 10 cm and the largest nest containing only 2,662 cells (Greene et al., *1976*). Conversely, one nest in 1973 (25 cm in diameter and 30 cm long) contained 4,277 cells, one in 1975 had 4,290 cells, and one in 1976 had 4,359 cells. Although the largest nests collected by Greene et al. (*1976*) had a maximum of six combs, Spencer (*1960*) mentioned two seven-combed nests from British Columbia. Adult worker populations during peak colony development vary from about 200 to 700, whereas total adult production of some colonies over the season may reach 6,500 or more. Table 4 shows colony composition in Pullman, Wash., for 1975. Colonies in Eastern States may average considerably smaller.

Commonly encountered nest associates of *D. arenaria* in southeastern Washington are the ichneumonid, *Sphecophaga vesparum burra*, the social parasite, *D. arctica*, and the pyralid moth, *Vitula edmandsae serratilineella* Ragonot (Greene et al., *1976*). The rate of parasitism by the ichneumonid was low, and did not seem to be an adverse factor in colony development. A diverse assortment of other arthropods, such as *Parcoblatta* sp. in nests in North Carolina and earwigs in nests in Washington, are probably incidental.

D. arenaria workers usually forage only for live prey, but may utilize carrion on occasion (Greene et al., *1976*). Searching patterns and the wide range of prey attacked indicate their foraging habits are quite similar to those of *V. pensyl-*

TABLE 4.—D. arenaria *colony composition in 1975, Pullman, Wash., and vicinity*[1]

Colony	Date	Workers	Queens	Males	Eggs	Larvae	Capped brood	Empty cells	*Sphecophaga* occupied cells	Multiple brood cells	Total cells	Combs
A-48	June 16	3	0*	0	74		11	0	0	0	85	2
A-49	16	4	0*	0	52		8	1	2	0	61	2
A-50	18	0	0*	0	34		5	0	0	0	39	1
A-51	21	5	0*	0	100		31	0	0	0	131	2
A-52	30	17	0*	0	214		34	0	0	1	248	2
A-56	July 17	316	0*	1	748		488	54	0	35	1,290	4
A-47	23	62	0*	0	416		153	2	0	0	571	3
A-57	Aug. 8	314	67	38	362	789	718	107	0	103	1,976	5
A-58	8	478	83*	0	309	792	854	176	0	11	2,131	5
A-59	12	295	0*	0	116	457	321	68	0	18	962	4
A-62	14	520	42	111	239	869	485	459	0	4	2,052	5
A-63	14	697	0*	188	296	1,346	668	546	16	89	2,872	5
A-47	Sept. 3	103	0	67	60	174	206	949	0	1	1,389	5
A-48	3	0	0	0	0	0	12	138	0	0	150	2
A-52	3	73	84	7	5	57	140	2,800	0	0	3,002	6
A-64	3	472	100	18	38	588	150	2,049	0	1	2,825	6
A-66	8	10	32	1	0	3	43	1,618	3	0	1,667	5
A-67	15	89	0	3	36	223	11	2,594	0	0	2,864	6

[1]Asterisk (*) indicates presence of foundress queen in addition to queen total given. Only one brood per cell tabulated; cells containing both larva and egg tabulated as larvae. Eggs and larvae not tabulated separately for first 7 colonies. Transplanted colonies A-47, A-48, and A-52 were analyzed twice (Greene et al., 1976).

vanica. Prey includes grasshoppers, spittlebug adults, leafhoppers, *Lygus* Hahn bugs, tree crickets, lacewings, caterpillars, flies, and spiders.

The behavior of *D. arenaria* within the nest was discussed by Greene et al. (*1976*). In many aspects, it is similar to that exhibited by other yellowjackets (Akre et al., *1976*); however, *D. arenaria* displays some important differences, including prey malaxation by the foundress queen for most of her life, prey malaxation by new queens and males, cap trimming by new queens, mauling of new queens by workers, and gastral vibration by the foundress queens and workers (table 3). Some of these activities have been observed in *D. maculata* colonies but not in other yellowjacket species.

D. arenaria workers do not ordinarily scavenge for protein and so are not usually serious picnic pests; however, like most yellowjackets, they may be attracted to sources of sugar in late summer. Isolated *D. arenaria* workers, apparently more so than other yellowjacket species, have an annoying and disconcerting tendency to buzz around the heads of people, sometimes following a person through the woods for a considerable distance. They may be foraging for flies, which often are found with any large animal. Since *D. arenaria* often constructs nests on manmade structures, the chances for encounters resulting in stings to humans are greatest in this situation. While small colonies may be quite mild and not easily aroused, larger colonies are formidable when disturbed. Attacking workers can even spray venom out of the sting (Greene et al., *1976*). Control of some *D. arenaria* colonies located in close proximity to human activity is therefore warranted.

Dolichovespula maculata

Dolichovespula maculata, the baldfaced "hornet," is an atypically large, black and white yellowjacket, which is probably the most widely distributed member of the Nearctic Vespinae. It occurs throughout the Canadian, Transition, Upper Sonoran, and Upper Austral Zones, and extends into the Lower Austral Zone (fig. 39). It has been collected virtually in every State and Canadian Province, from north-central Alaska to central Florida and the "Big Thicket" of southeastern Texas.

D. maculata queens first become active in April and May in southeastern Washington with nests usually established in late May or early June. Reproductives are produced in late July and August, and colonies enter decline in August or September. In the mid-Atlantic States, nest construction begins as early as late April. Nests are usually situated in vegetation, from shrubs or vines at ground level to 20 m or higher in trees. They may also be built on rock overhangs, electric power poles, houses, sheds, or other manmade structures (fig. 40 *b,d*). Nearly all are constructed in exposed locations, although Greene et al. (*1976*) mentioned literature reporting one subterranean nest and one inside a hollow tree.

Since *D. maculata* is a large wasp, its nests can sometimes attain impressive dimensions, with diameters of 35 cm and lengths of more than 60 cm (fig. 40*h*); however, much of the nest bulk is made up of thick, multilayered envelope, and the cells comprising the combs, although larger than those constructed by any other yellowjacket, are comparatively few in number. The most populous colonies construct 3,500 cells in five combs, but the majority of nests contain less than 2,000 cells in three or four combs. Peak worker population is typically 100 to 400, although one Maryland nest collected in mid-September contained 636 workers.

Nest associates of *D. maculata* have not been studied in detail. The ichneumonid *Sphecophaga vesparum burra* often occurs in low densities, and many of the incidental arthropods found with *D. arenaria* also have been collected in *D. maculata* nests. In Georgia and North Carolina, cockroaches (*Parcoblatta* sp.) are found in some nests. Recent investigations in Maryland suggest that a small chalcid wasp feeding on the brood may be important in limiting size and number of colonies in spring and early summer.

D. maculata workers occasionally scavenge for protein (Greene et al., *1976;* Payne and Mason, *1971*), but most forage only for live prey. Flies are commonly taken, and, in some areas, other yellowjackets are an important prey item (Howell, *1973*). One nest collected in Maryland contained the gasters of 44 *V. maculifrons*, 9 *V. squamosa*, 1 *V. flavopilosa*, and 1 honey bee, *Apis mellifera* L. The particulate detritus in this nest had a yellowish tone due to the extreme abundance of discarded yellowjacket parts and bits of integument. *D. maculata* workers are powerful, agile wasps and occasionally attack relatively large insects such as cicadas. There is even a report of an attack on an adult hummingbird (Grant, *1959*), although this is undoubtedly an unusual occurrence.

Although there are several papers on various aspects of the behavior of *D. maculata* (Balduf, *1954*; Gibo et al., *1974a,b*, *1977*; Rau, *1929*), a comprehensive sociobiological study of this species has only recently begun. Preliminary results indicate its behavior may be quite different from that reported for *D. arenaria*.

D. maculata has adapted to nesting in human population centers throughout its range, and can sometimes be found well within the boundaries of large cities. Its imposing size is often suffi-

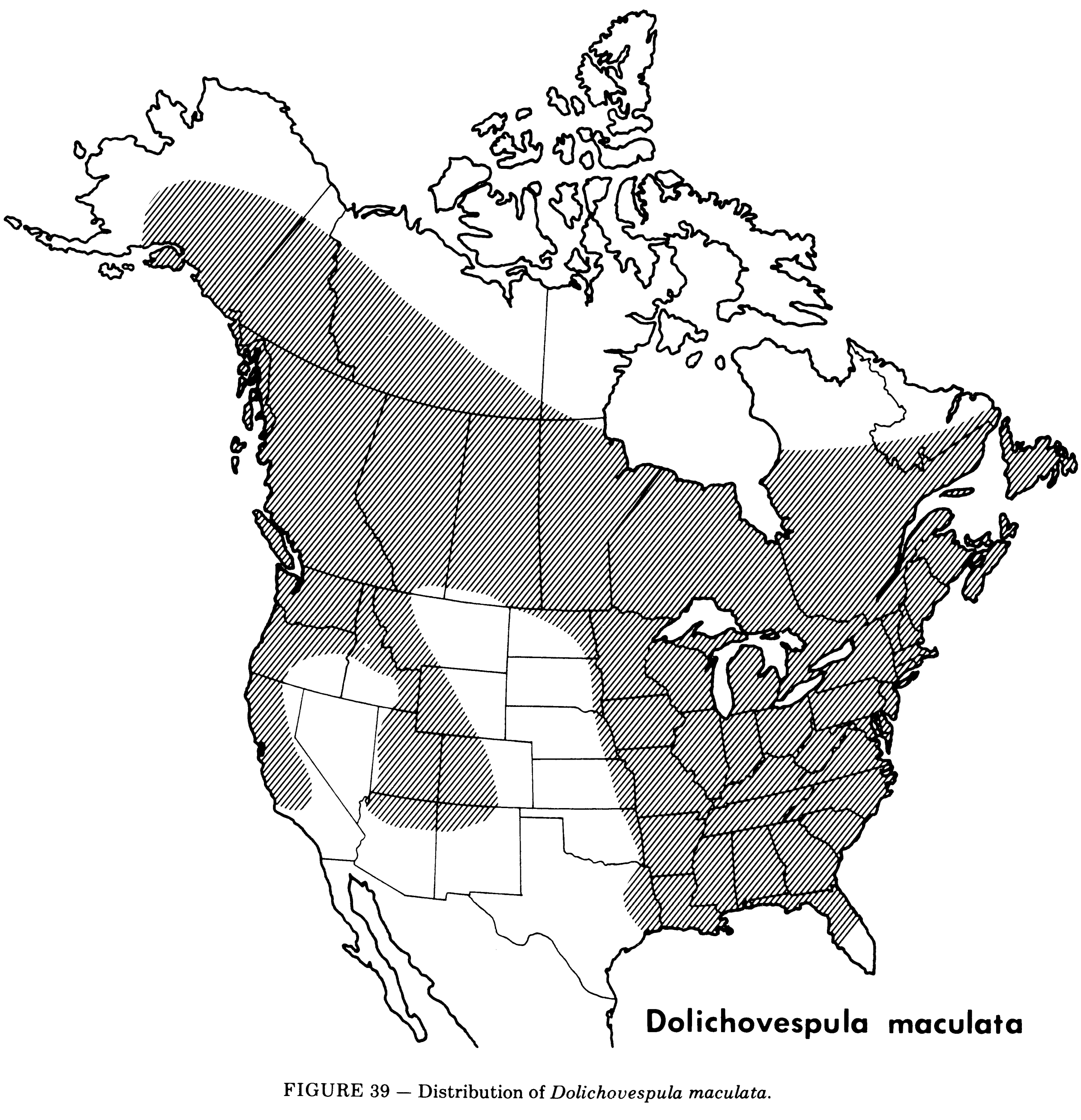
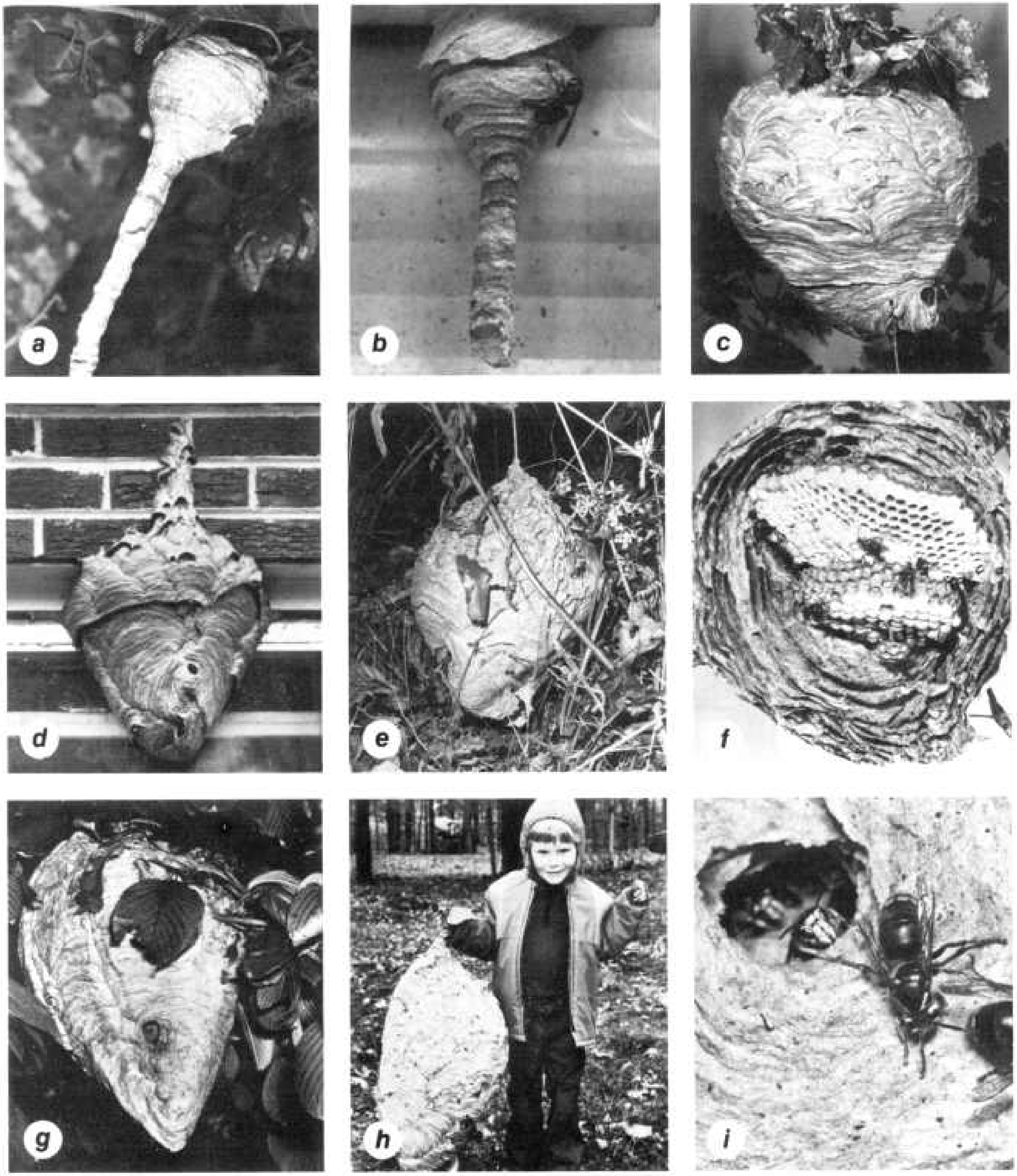


FIGURE 39 — Distribution of *Dolichovespula maculata*.



PN–6535

FIGURE 40 — *Dolichovespula maculata*: *a*, *b*, Queen nest with funnels 11 cm and 6.5 cm, respectively, La Grande, Oreg. (C.F. Roush); *c*, mature nest, Pullman, Wash.; *d*, mature nest on brick wall of house, Maryland; *e*, nest in weeds, Connecticut; *f*, nest with envelope removed exposing combs, Connecticut; *g*, mature nest fastened to tree branch, Connecticut (*e–g*, C.W. Rettenmeyer); *h*, nest 35 × 60 cm, Missouri (R. Oetting); *i*, workers around nest entrance, Connecticut (C.W. Rettenmeyer).

cient to alarm people, but its aggressiveness fortunately does not match its appearance. Although, as with any yellowjacket, accidental jostling of a nest or pressing on an individual will result in stings, our experience has been that workers are usually not as sensitive to disturbance around the nest as some of the other, smaller species. Furthermore, it has a tendency to nest fairly high in trees (more so than any other Nearctic wasp), reducing the likelihood of contact between humans and many colonies. The baldfaced "hornet" is often mentioned in introductory field biology guides, as much for its conspicuous architecture as its striking appearance, and is one of the handful of insects commonly recognized by laypersons. Its abandoned nests are displayed in almost every park nature center and sometimes hang as ornaments in homes. Unless a colony is located in close proximity to human activity, this species should not be regarded as a pest but rather as a colorful and beneficial part of the American insect fauna.

Dolichovespula norvegicoides

Dolichovespula norvegicoides is restricted almost entirely to the Canadian and Hudsonian Zones of the Boreal Region (fig. 41). Most aspects of the biology of this species are incom-

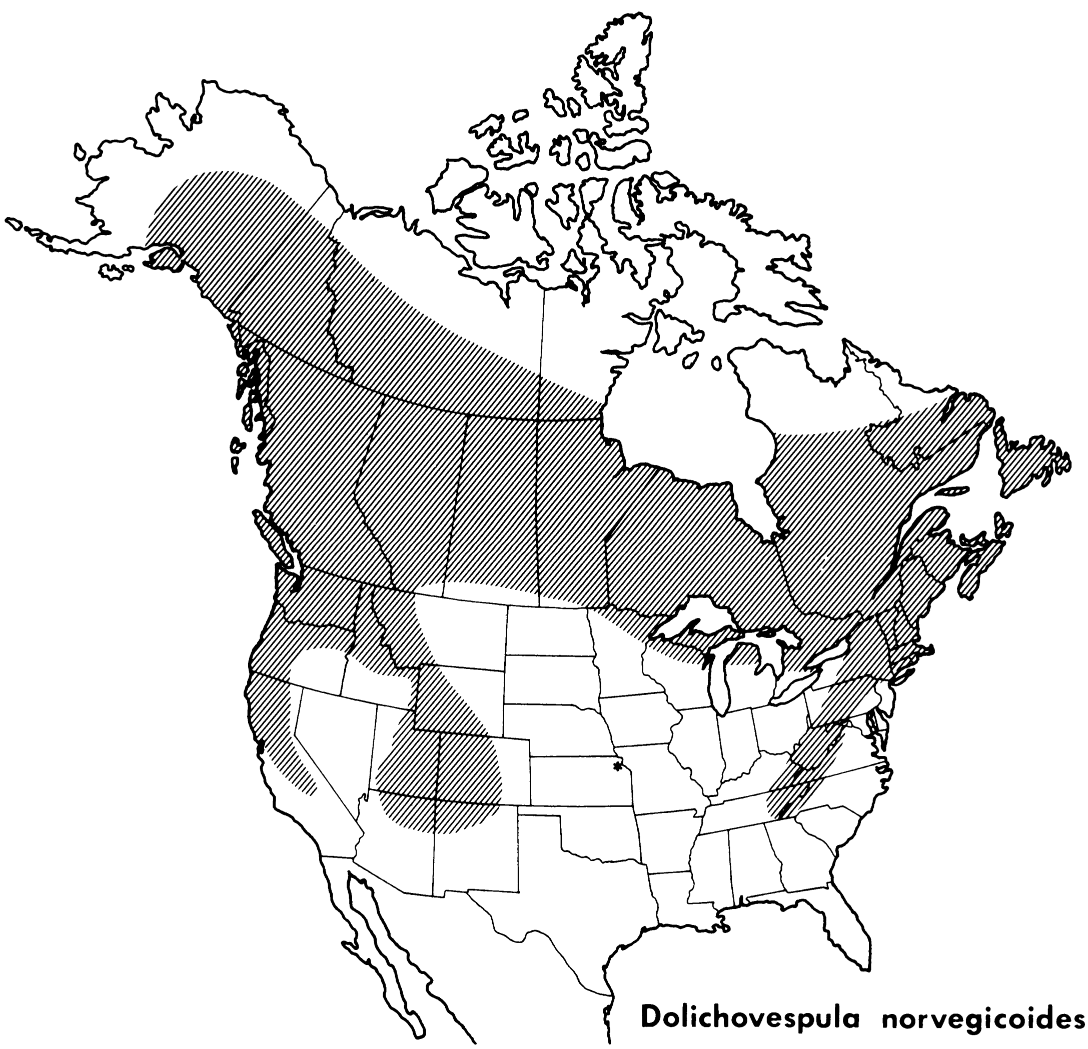


FIGURE 41 — Distribution of *Dolichovespula norvegicoides*.

pletely known and data on its behavior are totally lacking. The few recorded nests have been aerial and quite small. One examined in Vermont on August 6 by Bequaert (*1931*) was in dense bushes about 10 cm off the ground. The colony consisted of 50 workers and the foundress queen—reproductives had not yet emerged; however, Bequaert previously collected males in the Adirondacks as early as July 19. A nest collected in late October at Granite Lake in the Cabinet Wilderness, 10 to 15 miles south of Libby, Mont., was located in a shrub 15 cm above ground. The nest was 12.5 cm in diameter and had two combs with a total of 234 cells. Twenty-three dead workers were in the nest. Worker populations of *D. norvegicoides* probably seldom approach the size commonly attained by its close relative, *D. arenaria*.

R.E. Wagner (cited by Yamane, *1975*) reported the social parasite, *D. arctica*, is sometimes found in colonies of *D. norvegicoides*. Since there have been few collections, the incidence of parasitism is unknown.

Genus *Vespula*

Vespula rufa Species Group

The Nearctic members of the *V. rufa* species group include: *V. acadica*, *V. atropilosa*, *V. consobrina* (Saussure), *V. intermedia* (Buysson), *V. vidua* (Saussure), *V. austriaca*, *V. squamosa*, and *V. sulphurea* (Saussure). The first five species are a morphologically and biologically cohesive group; their taxonomic status has varied from treatment as varieties of the "parent" species, *V. rufa*, to full species (Miller, *1961*). The social parasite *V. austriaca* is closely related to its Palearctic host *V. rufa*, and there is no reason to treat it as other than a socially parasitic member of the *V. rufa* group. *V. squamosa* and *V. sulphurea* are of uncertain status (MacDonald et al., *1976*). The former is a frequent facultative parasite of *V. maculifrons*, a member of the *V. vulgaris* group. Since social parasites are usually closely related species, this casts doubt on the current placement of *V. squamosa* within the *V. rufa* group. The status of *V. sulphurea* is also uncertain because few data are available on its nesting biology and colony duration.

A number of superficial accounts of various aspects of the biology of *V. rufa* group species exist. The first and only detailed investigation of a *V. rufa* group species was of *V. atropilosa* in Washington. Other species have been studied somewhat, and only *V. intermedia* and North American *V. austriaca* remain unknown.

Vespula acadica.— *Vespula acadica* (forest yellowjacket) is restricted almost entirely to the Canadian Zone. (fig. 42).

V. acadica was reported as an aerial nester by Sladen (*1918*); however, two of three nests found by MacDonald et al. (*1975a*) were subterranean, and one was in a decaying log on the forest floor. From 1975 to 1977, eight additional nests were collected—six in forested areas near La Grande, Oreg., and two in northern Idaho near Harrison (Roush and Akre, *1978*). Four of these nests were in decaying logs, two were under logs, and the other two were subterranean, one in duff (partly decayed vegetable matter such as leaves and pine needles) and one in the soil (fig. 43). Entrance tunnels varied from 7 to 40 cm, usually 15 to 25 cm. The deepest subterranean nest was 15 cm under the soil surface. Nests were comprised of one worker-producing comb and one to three reproductive-producing combs. The largest mature colony consisted of 425 workers, 70 males, and 78 queens. The nest had four combs with a total of 1,791 cells. The seasonal cycle and size of the colonies were comparable to *V. atropilosa* colonies collected during the same year on comparable dates.

V. acadica workers prey only on live arthropods. They are predators on caterpillars, flies, and hemipterans. Other prey preferences are unknown.

No study of nest associates has been made, but five of the eight nests collected had 2 to 20 cells containing *Sphecophaga* cocoons, probably *S. vesparum burra*. A few nests had eggs of *Fannia* spp. on the outside envelope.

Being primarily a forest species, this yellowjacket has little contact with man; however, when colonies are disturbed, workers of this yellowjacket may be quite aggressive and persistent and sting repeatedly.

Vespula atropilosa.—*Vespula atropilosa* (prairie yellowjacket) is found in western North America where it is restricted to the Canadian and Transition Zones of the Boreal Region (fig. 44). Detailed biological and behavioral investigations were reported by Akre et al. (*1976*) and MacDonald et al. (*1974, 1975a. 1975b*).

V. atropilosa is abundant in prairie and open forest areas, but becomes increasingly less abundant in heavy forest where it is replaced by *V. acadica*. It also commonly nests in yards, pastures, golf courses, and similar areas.

V. atropilosa was reported as a subterranean nester by Bequaert (*1931*), Bohart and Bechtel (*1957*), Buckell and Spencer (*1950*), and Miller (*1961*). MacDonald et al. (*1974, 1975a*) reported locations of 40 nests of *V. atropilosa* near Pullman, Wash. Thirty-six were subterranean, and the remaining four were in various locations —under sod pile, inside decayed 4- by 4-inch timber (fig. 45*f*), in tree hollows, and beneath steps. From 1974 to 1977, an additional 55 colonies were located; 3 were nesting in between walls of hous-

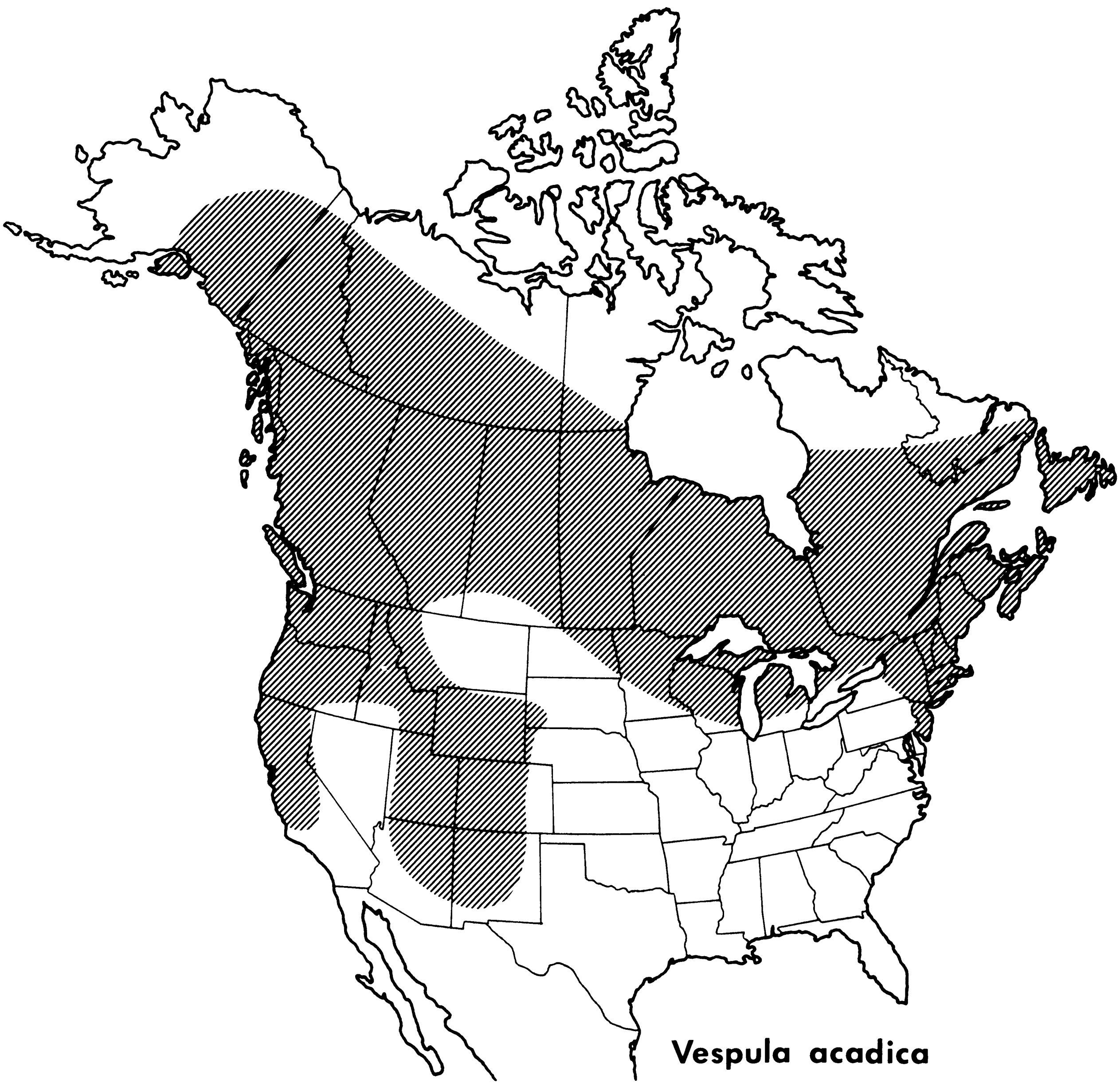


FIGURE 42 — Distribution of *Vespula acadica*.

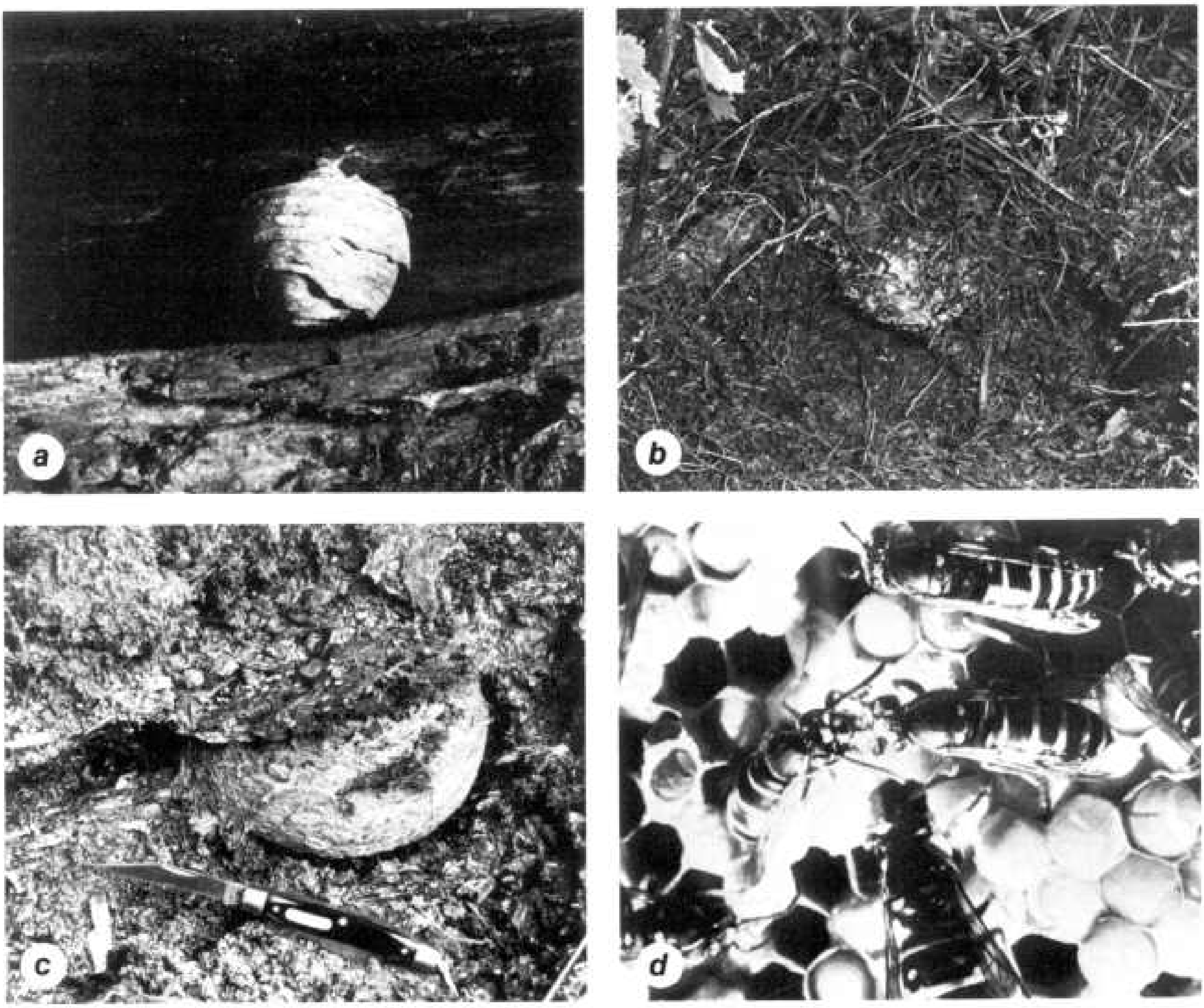
es, and the other nests were subterranean. Most nests were built in rodent burrows with the nest located 10 to 30 cm into the tunnel and 10 to 15 cm below the soil surface.

In the spring of 1977, an old (1976) nest of *V. atropilosa*, containing 730 cells in 2 combs, was found in a truly aerial position in Pullman. The nest was 150 cm above the ground—located underneath a concrete overhang, which was part of some steps—and was fastened to concrete on two sides and to plywood on the top.

Table 5 compares mature (with reproductive cells) *V. atropilosa* colonies from 1971 to 1975. All colonies collected during 1976-77 were ex-

TABLE 5.—*Comparison of mature colonies (with reproductive cells) of* Vespula atropilosa, *1971-75*

Year	Nests	Cells in smallest nest	Cells in largest nest	Average number of cells per nest	Most workers collected per colony
			Number		
1971	6	942	2,676	1,890	368
1972	5	484	1,068	884	76
1973	16	549	2,175	1,236	270
1974	14	603	2,497	1,313	504
1975	13	278	1,556	897	484



PN-6536

FIGURE 43 — *Vespula acadica*: *a*, Queen nest in hollow log, Laird Park, Idaho; *b*, nest in pine needles and duff of forest floor, Harrison, Idaho; *c*, nest in decayed tree root, La Grande, Oreg. (C.F. Roush); *d*, workers in trophallaxis on comb of nest.

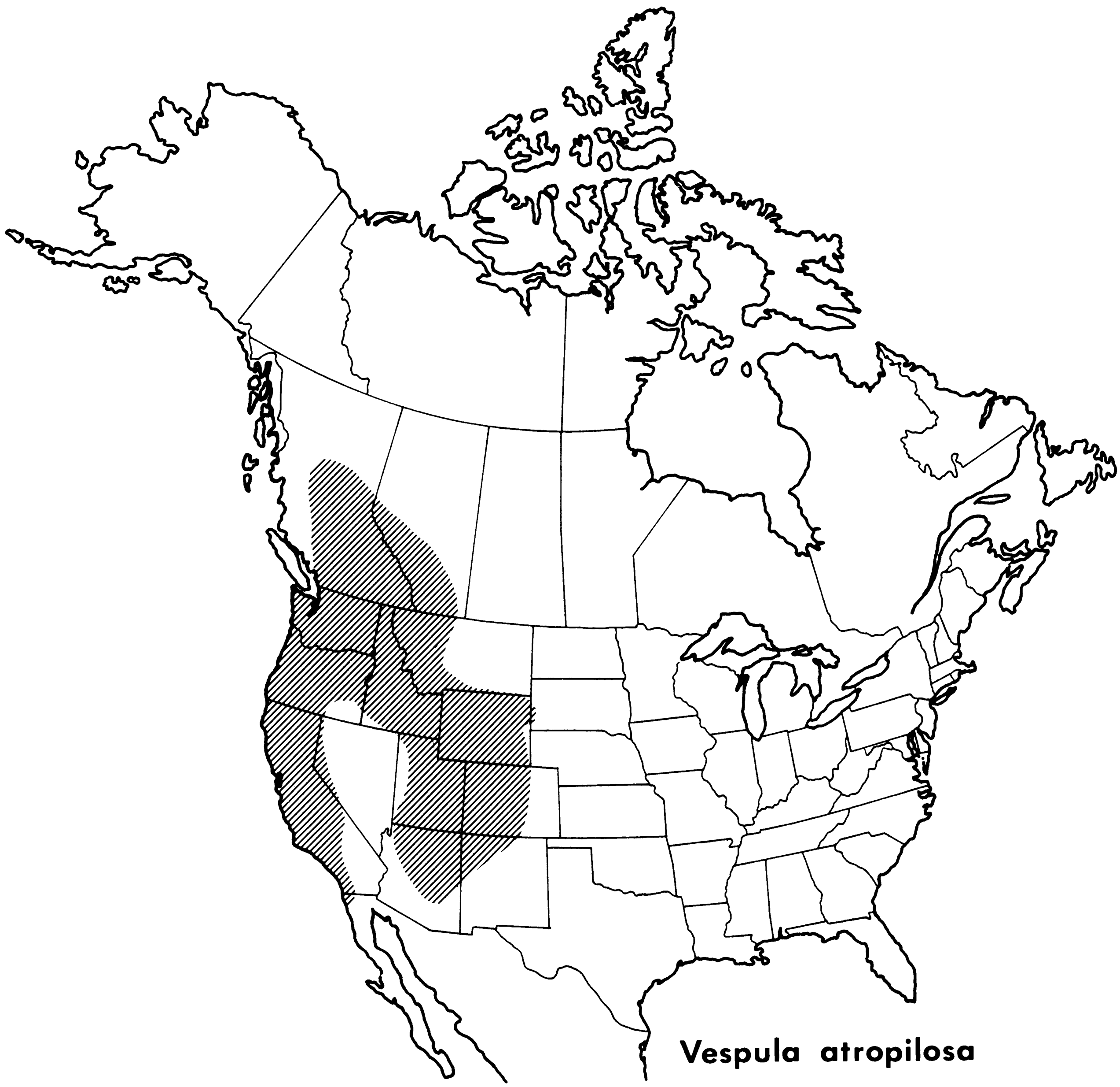
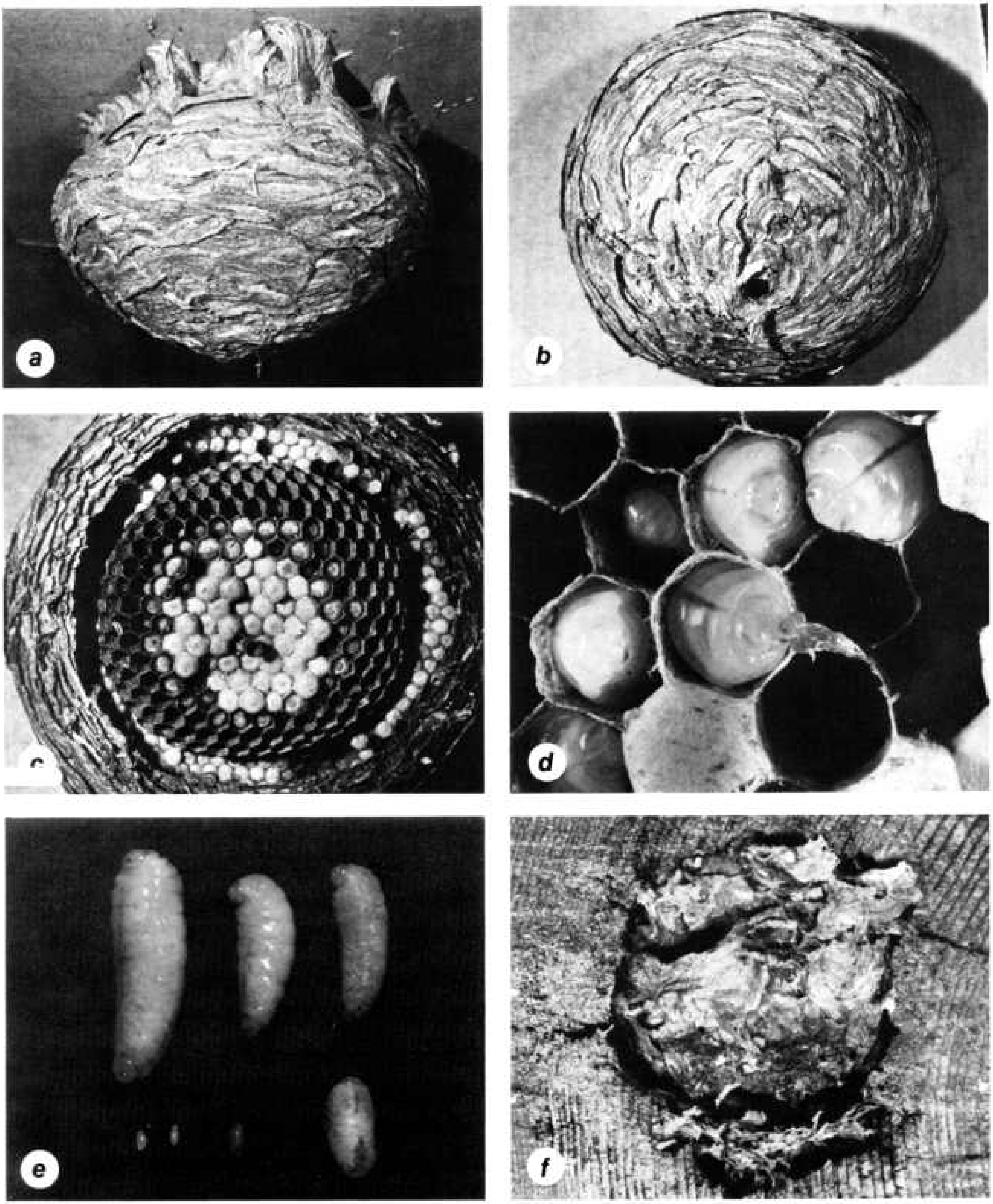


FIGURE 44 — Distribution of *Vespula atropilosa.*

cluded as they were used in experiments. Nest size varied from year to year with the nest of the smallest mature colony comprised of 278 cells; the largest, 2,676. When collected, the greatest number of workers in a colony was 504. This is typical of colonies and nests of all members of the *V. rufa* group, which are only one-fifth to one-fourth as large as those of members of the *V. vulgaris* group (table 1).

V. atropilosa workers are predators only on live prey. They often attack spiders, phalangids, flies, caterpillars, hemipterans, and some homopterans, but seldom attack other Hymenoptera or beetles.

Nest associates of *V. atropilosa* were studied by MacDonald et al. (*1975b*). Most associates are scavengers in debris below the nest or on fungi growing on the nest carton. Nests of *V. atropilosa* are quite filthy, with remnants of bodies and other debris incorporated into the



PN-6537

FIGURE 45 — ***Vespula atropilosa***: *a–c*, Nest built in cardboard box in shed; *b*, ventral view; *c*, envelopes removed; *d*, mature larva chewing on insect flesh; *e*, egg, larvae, prepupa; *f*, nest in hollow 4 × 4 inch beam.

nest envelope and carton, probably providing scavengers still another supply of food. The pupal parasite, *Sphecophaga vesparum burra*, appears to adversely affect development of young colonies. This is an abundant species and some colonies invariably nest in yards, causing homeowners concern and often warranting removal; however, workers are usually no problem unless the colony is disturbed.

Vespula austriaca.—*Vespula austriaca*, a rarely collected species, is widespread throughout the Boreal Region of North America (fig. 46). An obligatory social parasite of Palearctic *V. rufa*, *V. austriaca* does not possess a worker caste and is dependent on host workers to rear its brood of new males and queens. Various workers (Carpenter and Pack-Beresford, *1903*; Pack-Beresford, *1904*; Sharp, *1903*; Weyrauch, *1937*) described certain aspects of the biology of *V. austriaca* and its host *V. rufa* as summarized in Spradbery (*1973a*).

V. austriaca is sympatric with a number of potential *V. rufa* group hosts (Miller, *1961*); however, our studies indicated that *V. acadica* was the most likely host. During the summer of 1978, two colonies of *V. acadica*, each with a *V. austriaca* queen, were collected in northern Idaho near the small town of Harvard. These are

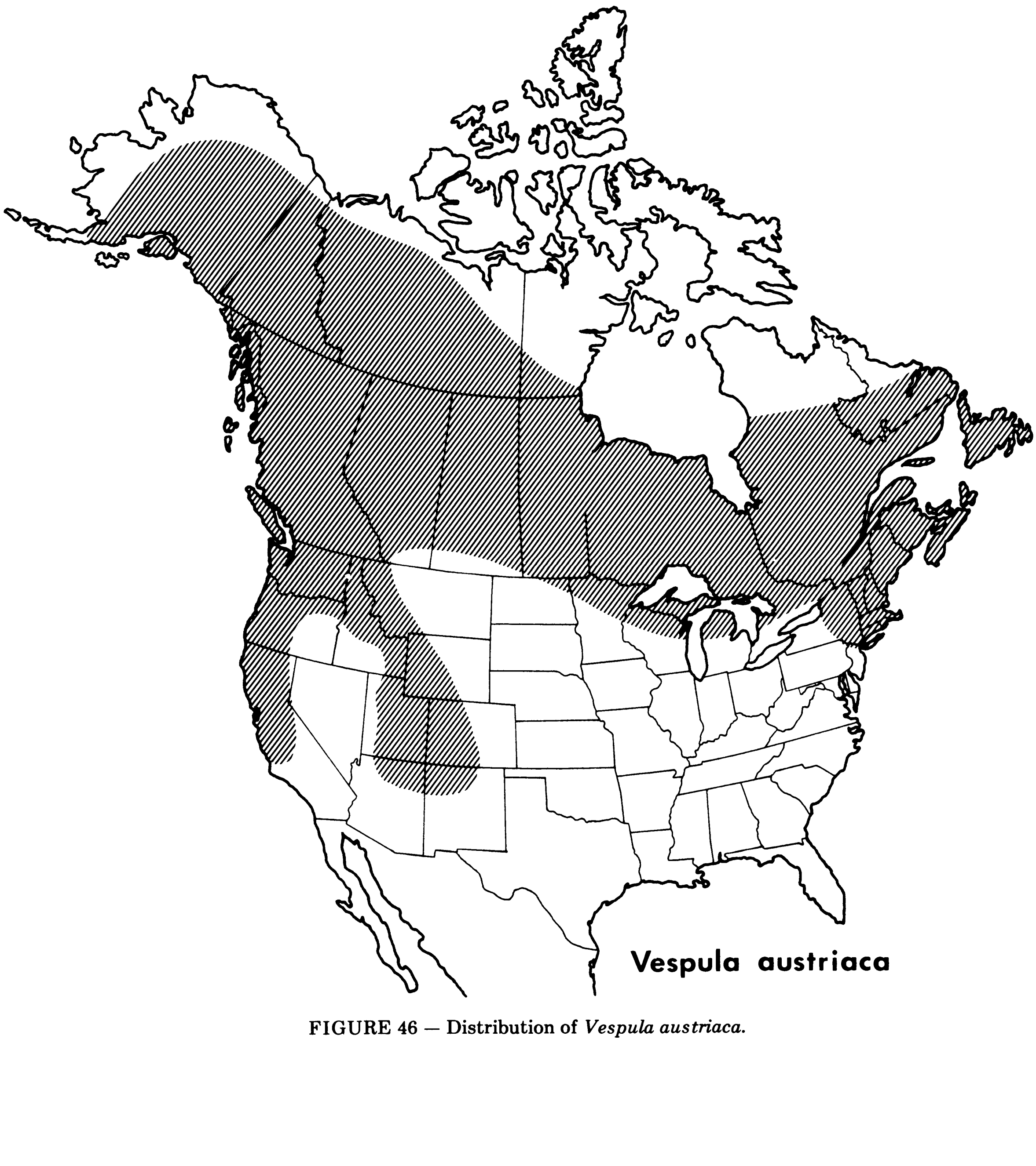


FIGURE 46 — Distribution of *Vespula austriaca.*

the first records of this social parasite being taken from nests of a Nearctic yellowjacket (Reed et al., *1979*).

Vespula consobrina.–*Vespula consobrina* (blackjacket) is a black and white yellowjacket found in forested areas throughout the Canadian and Transition Zones of the Boreal Region of North America (fig. 47). Nests are typically in subterranean rodent burrows but may be aboveground in logs or rock cavities (MacDonald and Matthews, *1976*) or in the walls of houses (Gaul, *1948*). Five of nine nests located in Washington during 1974-77 were in rodent burrows, the remaining four were in the walls of buildings.

The colony cycle is short like that of other *V. rufa* group species, with colonies declining and producing reproductives by mid-September in Pullman and by September 1 in North Carolina (MacDonald and Matthews, *1976*). *V. consobrina* colonies are small; the average size of four

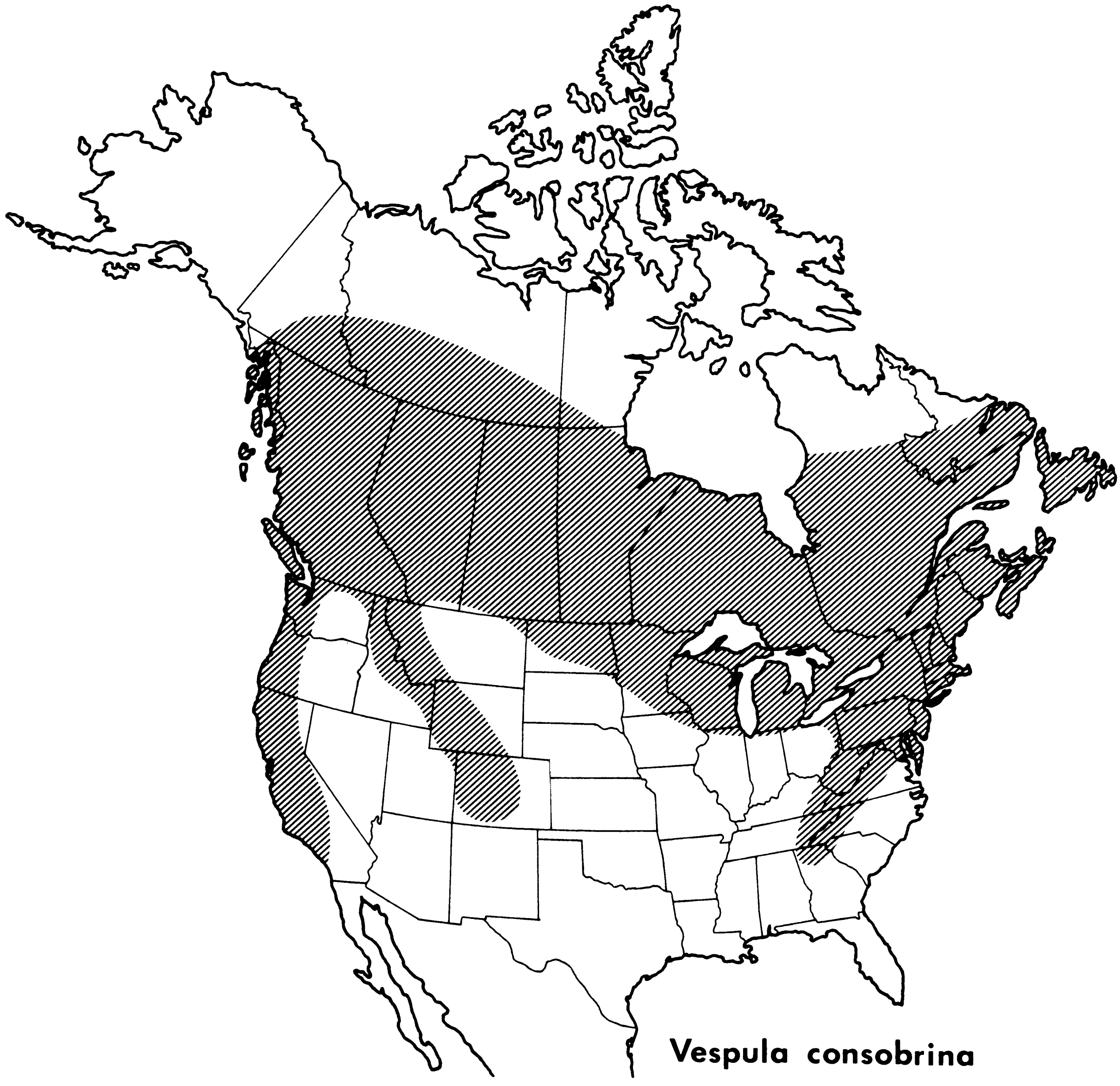


FIGURE 47 — Distribution of *Vespula consobrina*.

mature nests collected in Pullman in 1974 was only 555 cells, ranging from 490 to 690 cells (fig. 48). MacDonald and Matthews (*1976*) reported on two North Carolina colonies with 1,437 and 731 cells with less than 100 workers per colony. Other reports also indicate the small size of *V. consobrina* colonies (Dow, *1930*; Gaul, *1948*; Taylor, *1939*). Nests consisted of one worker-producing comb and from one to three reproductive-producing combs.

The little information available indicates a lesser incidence of nest associates with *V. consobrina* colonies than with *V. atropilosa*; however, one colony collected in Pullman in 1974 contained 33 adult phorid flies (*Triphleba lugubris*); 28 were gravid females. Both North Carolina colonies harbored eggs and larvae of *Dendrophaonia querceti* and *Fannia* spp. (Diptera: Muscidae).

V. consobrina colony development and social behavior are not well known, but studies indicate they are similar in most respects to that reported for *V. atropilosa* by Akre et al. (*1976*). Foraging is for live prey only, with spiders and phalangids readily accepted. Other arthropods utilized as prey are similar to those attacked by *V. atropilosa.*

Regarding interspecific interactions, one instance of colony "drift" was recorded when several *V. consobrina* workers joined a *V. atropilosa* colony where they oviposited as evidenced by the production of numerous *V. consobrina* males later in the season (Akre et al., *1976*). *V. consobrina* workers appear aggressive in interactions with other *Vespula* spp. workers. For example, a single worker successfully fended off many *V. pensylvanica* workers at a dish of honey and usually chased them away.

As with other *Vespula* spp., aggressiveness varies considerably relative to colony size and history. Some are distinctly more easily aroused to sting than others although Gaul (*1948*) regarded *V. consobrina* as not aggressive. Because of its infrequent contacts with man, this species poses little problem for humans in most areas of North America; however, in forested areas of western North Carolina, the blackjacket is responsible for numerous stinging episodes among loggers.

Vespula intermedia.—*Vespula intermedia*, a black, ivory, and red species, is restricted almost entirely to the Hudsonian Zone of the Nearctic Boreal Region (fig. 49). It is rarely collected, and no nest has been found (Miller, *1961*). Since other members of the *V. rufa* group are attracted to synthetic organic compounds such as heptyl butyrate, use of attractant traps might be of value in surveying for this species.

Vespula vidua.—*Vespula vidua* is restricted almost entirely to the Transition and Upper Austral Zones of eastern North America (fig. 50). The nesting biology of this species was studied by MacDonald and Matthews (*1976*), but detailed behavioral information is lacking.

Seemingly less restricted to forested habitats than *V. acadica* and *V. consobrina*, *V. vidua* commonly nests in disturbed areas (yards, pastures) as well as forests from Minnesota and

PN-6538

FIGURE 48 — *Vespula consobrina*: *a*, Mature nest; *b*, nest, envelope removed.

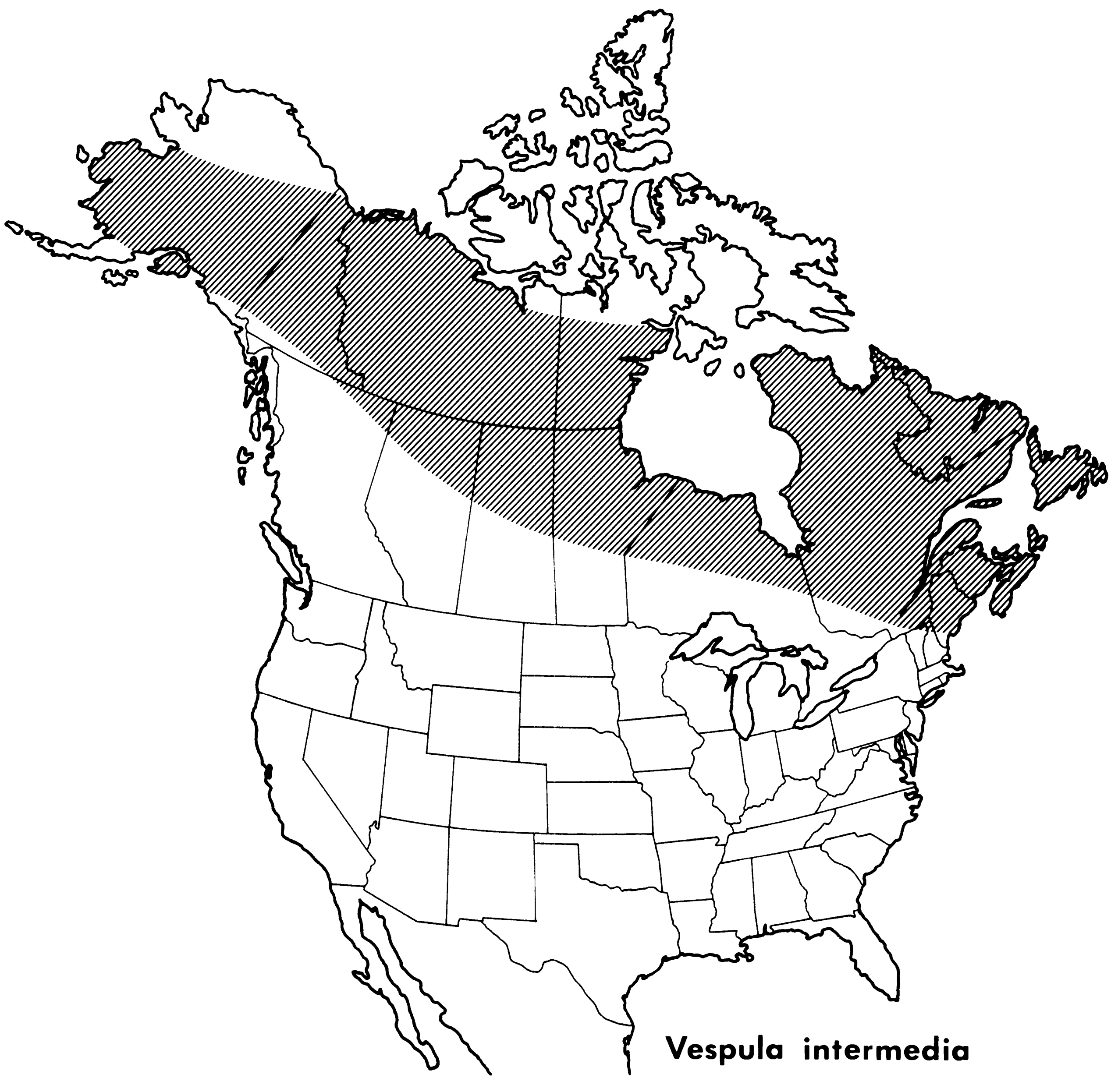


FIGURE 49 — Distribution of *Vespula intermedia.*

Iowa to the New England States, then south into northern Georgia. The relative abundance of *V. vidua* in many of these areas is unknown. In many respects—nest habitats and locations, size and architecture (fig. 51), seasonal duration and size of colonies, adult size—*V. vidua* is the eastern counterpart of *V. atropilosa.* Indeed, without the presence of adults or developed pupae, a nest of *V. vidua* cannot be distinguished from a nest of *V. atropilosa.*

Although most nests of *V. vidua* are subterranean, it has also been reported as nesting in decaying logs (MacDonald and Matthews, *1976*), and in manmade structures (Ebeling, *1975*, and Shew[2]). The seasonal cycle of *V. vidua* is short as is common for *V. rufa* group members. The

[2]Shew, R.L. The biology and control of vespine wasps. M.S. thesis, Ohio State University. 59 pp. 1966. [Mimeographed.]

largest colony (six analyzed) constructed a nest of 2,447 cells and had an estimated adult worker population of 385 at its peak of development (MacDonald and Matthews, *1976*). Nests consisted of one worker-producing comb and from one to three reproductive-producing combs.

Although Wagner and Reierson (*1971a*) reported *V. vidua* workers as pests around picnic tables, they were probably capturing insects in the area or momentarily attracted to odors. This species is not a stinging hazard to humans unless the nest is located in structures or yards where the colony can be disturbed by human activities.

Uncertain Status of *Vespula squamosa* and *V. sulphurea*

These two species are unique among yellowjackets in possessing a characteristic mesonotum with two long, broad, longitudinal yellow

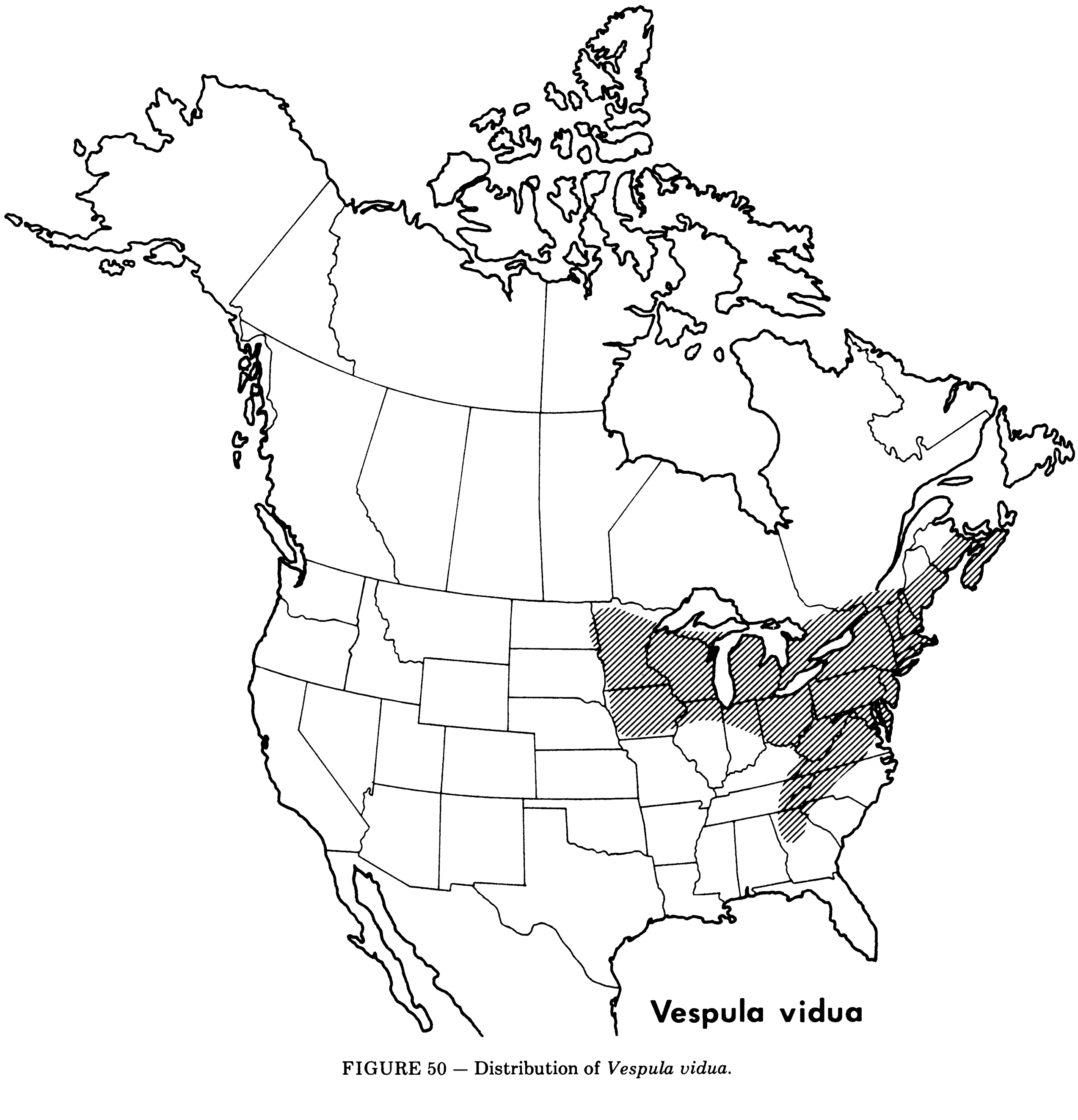
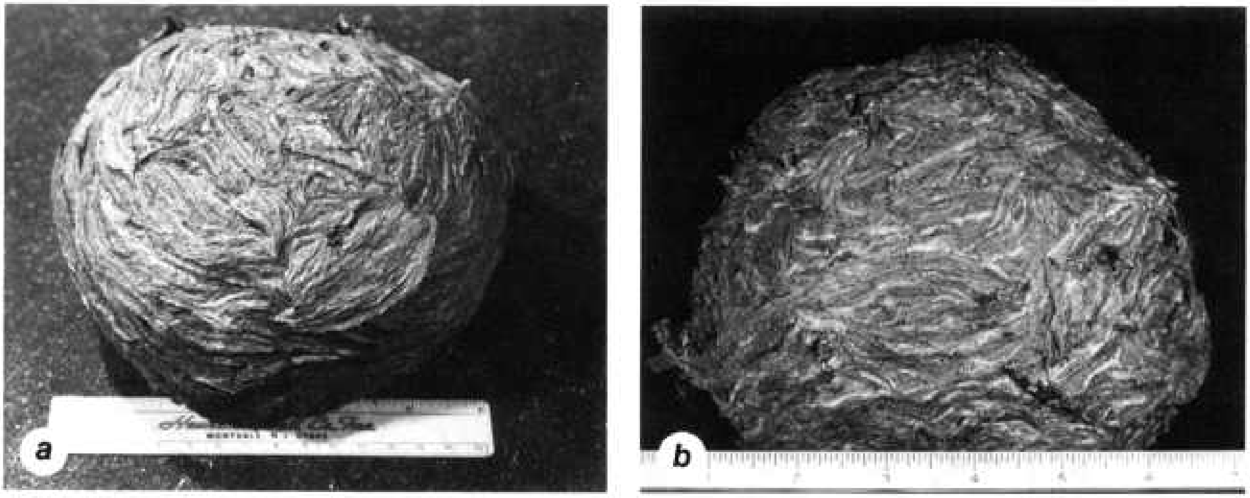


FIGURE 50 — Distribution of *Vespula vidua*.



PN-6539

FIGURE 51 — *Vespula vidua*: *a*, Mature nest taken from honey bee nest box, New York (R. Keyel); *b*, mature nest, North Carolina.

stripes. Accordingly, they have been considered closely related (Duncan, *1939*), and united with the *V. rufa* species group on the basis of adult morphology (Bequaert, *1931*). Studies have now shown that both species have seven ovarioles whereas other members of the *rufa* group, members of the *vulgaris* group, and four *Dolichovespula* spp. have only six ovarioles (Kugler et al., *1976*). Biological study of *V. sulphurea* is totally lacking, and *V. squamosa* has only recently received attention (MacDonald and Matthews, *1975, 198__b*). These studies revealed *V. squamosa* differs from other *V. rufa* group members in a number of ways, including seasonal duration and size of colonies, nest size and architecture, and, possibly, foraging behavior. Indeed, *V. squamosa* appears more similar biologically to the *V. vulgaris* group.

Unfortunately, little data are available on *V. sulphurea*, but it may share biological as well as morphological attributes with *V. squamosa*. Indepth behavioral studies are needed, and until then we prefer to consider these two species as of uncertain status.

Vespula squamosa.— *Vespula squamosa* (southern yellowjacket) is widely distributed from Iowa to Texas and across to the eastern seaboard, and occurs in the southeastern part of the Transition, Upper Austral, and Lower Austral Zones of the Nearctic Region (fig. 52), and also in southern Mexico and Guatemala. Nesting biology was studied by MacDonald and Matthews (*1975, 198__b*).

Easily recognized by its color pattern and extreme female caste dimorphism, *V. squamosa* is an intriguing species. Unassociated until the early 1900's when a colony was excavated, the very large and predominately orange queen differs markedly from the worker and male, which are more typical of yellowjackets in size and color. Also curious is the success of *V. squamosa* in the southern distribution of Nearctic *Vespula*. Since the discovery of a *V. squamosa* queen in the nest of *V. vidua* (Taylor, *1939*), *V. squamosa* has been considered a facultative social parasite of *Vespula*.

Working in Georgia, MacDonald and Matthews (*1975*) found *V. squamosa* to be a facultative social parasite of *V. maculifrons*, a member of the *V. vulgaris* group. The parasite queen usurps the nest from the host queen and assumes complete control of the colony. Host workers rear the first brood of *V. squamosa* workers and eventually a colony consisting solely of *V. squamosa* results. The relationship appears to be facultative since about 20 percent of mature *V. squamosa* colonies exhibit no evidence of a *V. maculifrons* heritage. The remaining 80 percent either contain host workers (early in the season) or the nests have clearly visible remnants of *V. maculifrons* nest construction. The incipient host nest with much smaller, tan cells is in striking contrast to the surrounding larger, gray cells constructed by parasite workers; thus, although host workers may not be present, the early history of a *V. squamosa* colony can be determined by analyzing nest architecture.

The above account depicts the host-parasite relationship in Georgia. In other areas, a different host species may be involved, and the percentage of nests parasitized probably varies considerably. Accordingly, discussion of the nesting biology of *V. squamosa* must take into account the requirements of host species.

Most *V. squamosa* colonies (usurped or pure) are located in disturbed habitats, particularly in yards, parks and roadsides, whereas a few are in "natural" habitats. Among the latter, nearly all colonies are in pine forests, a few are in mixed

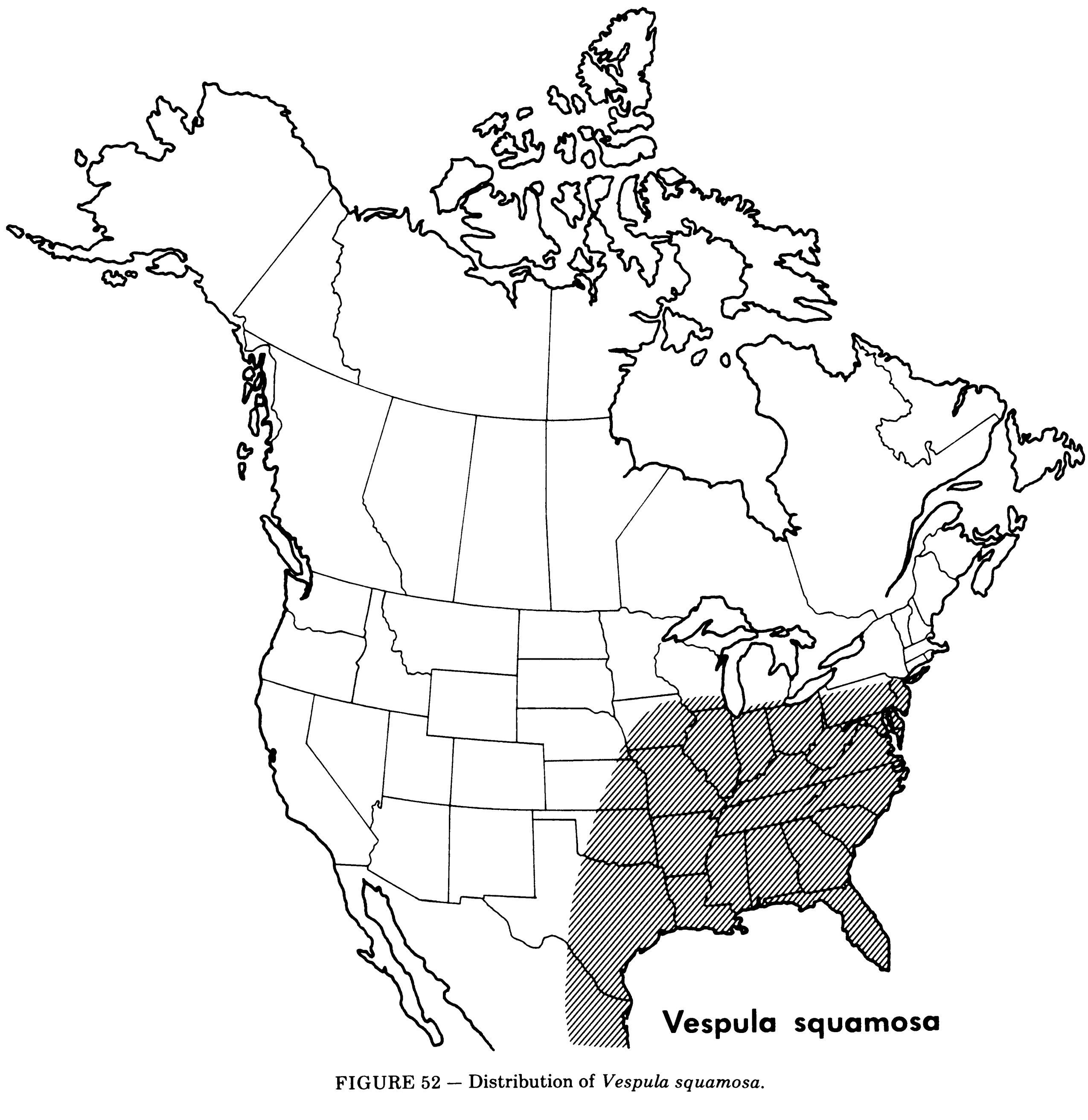


FIGURE 52 — Distribution of *Vespula squamosa*.

forests but rarely in hardwoods despite the abundance of *V. maculifrons* colonies.

Coincident with its host, *V. squamosa* nests typically are subterranean (MacDonald and Matthews, *1975, 198__b;* Miller, *1961*); however, aerial nests have been reported (Tissot and Robinson, *1954*), and in the Washington, D.C., area where *V. maculifrons* commonly nests in house walls, *V. squamosa* colonies are also frequently observed in these locations. Colonies typically persist into autumn with most producing reproductives from late August into November; this seems intermediate between the longer cycle of the *V. vulgaris* group and the shorter cycle of the *V. rufa* group. Colony size is variable but most contain 500 to 4,000 workers at their peak and ultimately construct a nest of 2,500 to 10,000 cells (table 6).

Sometimes, perennial colonies of this species persist in subtropical areas of its distribution. For example, Tissot and Robinson (*1954*) recorded a nest of *V. squamosa* of 6 ft by 30 inches by 12 inches with 17 combs, and another was 9 ft tall with a circumference of 9 ft 10 inches and contained 39 combs. A perennial, subterranean colony located 13 miles west northwest of Gainesville, Fla., was killed in early February 1977 (J. Sharp, USDA, SEA, Gainesville). The nest had 14 comb levels and 120,130 cells (fig. 53 *a, b*); at least 1,350 of these cells were reproductive cells, although a complete count could not be made because of the nest's poor condition.

Although the behavior of *V. squamosa* has not been studied, some of the workers definitely scavenge for protein (R. Matthews, Univ. of Ga., personal commun.) and may be a nuisance at picnics. This behavior is not typical for *V. rufa* group species.

V. squamosa is an important pest species because of the great number of nests found in urban and recreational areas. Colonies are typically large and disturbances of the nests usually result in multiple stings.

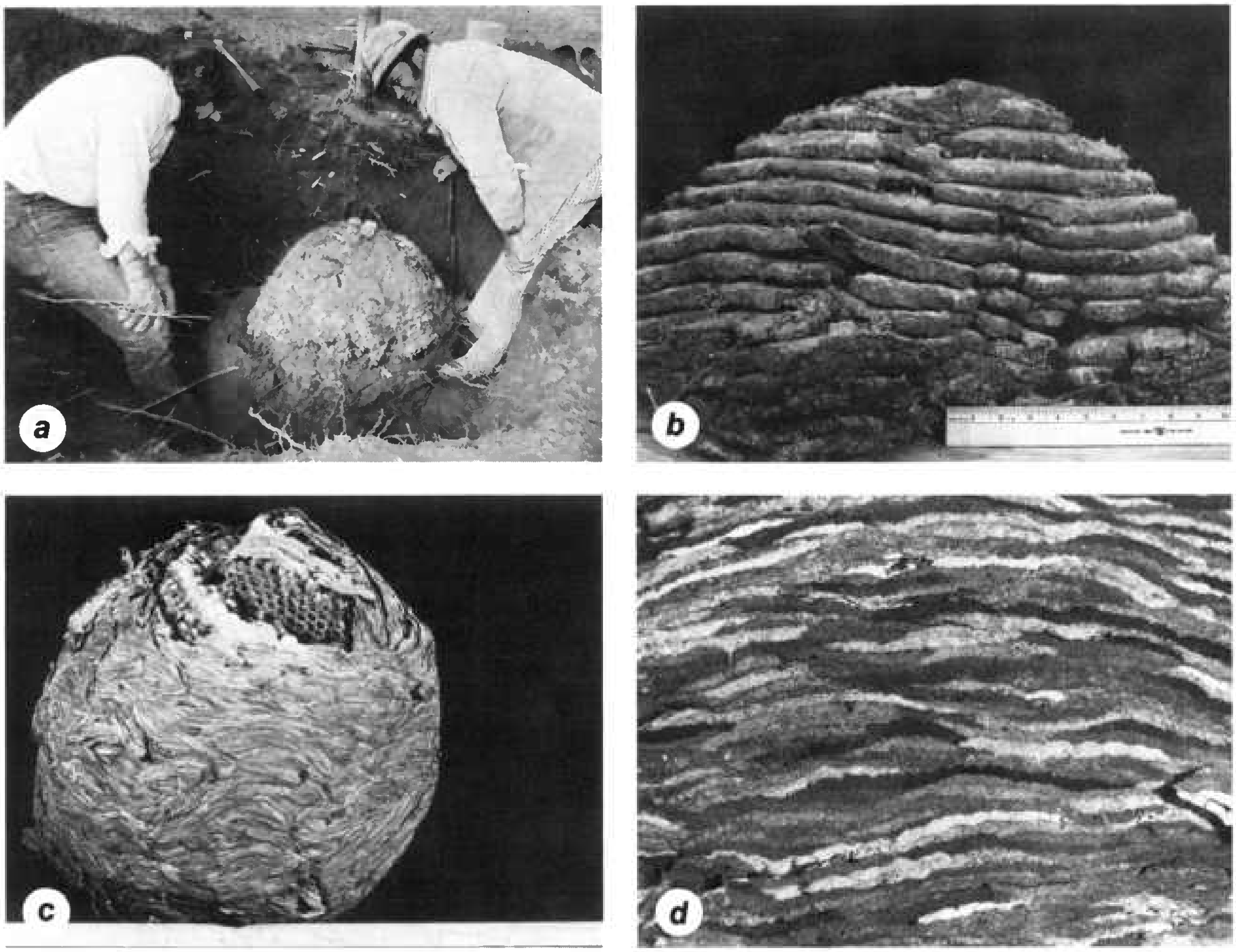
Vespula sulphurea.—*Vespula sulphurea* (California yellowjacket) is restricted almost entirely to the Upper Sonoran fauna of California, but it also occurs in southern Oregon, western Nevada, southern Arizona, and northern Baja, Mexico (fig. 54; Bohart and Bechtel, *1957*). Duncan (*1939*) mentioned three nests that he collected, and included several photographs of one.

Based on the limited data available, *V. sulphurea* is a subterranean nester. One of the colonies collected by Duncan (*1939*) in early October 1930 was comprised of 134 workers, 6 new queens, and the foundress queen. The nest contained a few male pupae. Seven additional subterranean colonies have been collected in California by R. E. Wagner (Univ. of Calif., Riverside) (table 7). Three nests had three worker combs, two of these also had a single primary reproduc-

TABLE 6.—*Summary of mature* Vespula squamosa *colonies collected after October 15, 1974-75, in and around Athens, Ga. (MacDonald and Matthews,* 198__a)

Parameter	1974		1975	
Colonies located	[1]75		[2]46	
	Largest	Average	Largest	Average
Total cells per nest	9,906	5,703 (N = 26)	9,802	5,034 (N = 9)
	Average	Percent of total cells	Average	Percent of total cells
Queen cells per nest	1,001 (N = 26)	17 percent	842 (N = 9)	19 percent
Maximum workers per colony	3,697		3,193	
Combs per nest	Average		Average	
Worker	4.5		3.9	
Mixed	0.6		0.6	
Queen	2.3		2.0	
Total	7.1		6.3	

[1]Of 75 *V. squamosa* colonies excavated, 62 were initially founded by *V. maculifrons.*
[2]Of 39 *V. squamosa* colonies excavated, 37 were initially founded by *V. maculifrons.*



PN–6540

FIGURE 53 — *Vespula squamosa*: *a*, Excavation of perennial nest 13 miles west-northwest of Gainesville, Fla., Feb. 2, 1977, by J. Ryan, left, and J. James, right (J.F. Sharp); *b*, same nest, envelope removed exposing combs; *c*, mature nest, Athens, Ga.; *d*, atypical nest envelope with highly colored stripes; most nests are uniformly gray.

tive-cell comb. Partial reproductive combs are often placed wherever space is available in the nest, even adjacent to the first worker comb; however, no reproductive cells have been found on worker combs.

"This species has a slightly shorter active season than *V. atropilosa*, the first workers appearing a week or so later and the last workers disappearing a couple of weeks before those of *V. atropilosa*" (R. E. Wagner, personal commun.).

Workers of *V. sulphurea* are attracted to heptyl butyrate, but other aspects of their behavior are unreported. Members of this species are not very abundant, and workers have not been reported as picnic pests.

Vespula vulgaris Species Group

The Nearctic members of the *V. vulgaris* group include *V. vulgaris*, *V. flavopilosa*, *V. maculifrons*, and *V. pensylvanica*. A fifth species, *V. germanica*, was introduced into the United States (Menke and Snelling, *1975*), has recently become abundant in the East, and appears to be gradually spreading westward across the country (Morse et al., *1977*).

Workers of the *V. vulgaris* group species are notorious scavengers and frequently are pestiferous to man, especially in recreation areas and at outdoor picnics. Accordingly, these important pests have been investigated much more than

FIGURE 54 — Distribution of *Vespula sulphurea.*

other *Vespula* spp. European species have been studied in detail by a number of investigators (Spradbery, *1973a*), as have some of the Oriental species (Iwata, *1976*). Biological investigations in America were reported by Akre et al. (*1975, 1976*), Duncan (*1939*), Jacobson et al. (*1978*), MacDonald et al. (*1974, 1975a, b, 1976, 1980*), MacDonald and Matthews (*198_a*), and Preiss.[3]

[3]Preiss, F.J. Nest site selection, microenvironment and predation of yellowjacket wasps, *Vespula maculifrons* (Buysson), (Hymenoptera: Vespidae) in a deciduous Delaware woodlot. M.S. thesis, University of Delaware. Newark. 81 pp. 1967. [Mimeographed.]

TABLE 7.—*Summary of* Vespula sulphurea *colonies collected in California (After R.E. Wagner)*

Colony No.	Locality	Date collected	Adults: Workers	Adults: Queens	Adults: Fall queens	Adults: Males	Worker combs and No. cells	Reproductive combs and No. cells
			----- *Number* -----					
1	Clear Lake	7-27-72	580	1	0	0	([1])	([1])
2	Clear Lake	9-11-72	804	0	23	287	([1])	([1])
3	Clear Lake	9-12-72	1,086	1	31	363	3 – 3,258	1 + 4 partial – 769
4	Clear Lake	9-13-73	392	1	7	44	([1])	([1])
5	Clear Lake	9-24-72	556	0	103	258	([1])	([1])
6	Malibu Canyon, Santa Monica Mountains	7-03-75	462	1	0	0	3 – 1,641	0 – 0
7	Mill Creek, San Bernardino Mtns.	8-27-75	105	1	0	0	3 – 1,080	1 – 33

[1]Not available.

Vespula flavopilosa.—*Vespula flavopilosa* (hybrid yellowjacket) occurs from Minnesota to the east coast and south to northern Georgia (fig. 55). Future collection records will undoubtedly extend this known distribution.

Similar to *V. maculifrons* and *V. vulgaris* in most aspects of its biology, *V. flavopilosa* constructs subterranean nests (fig. 56) of tan, fragile carton (not gray carton as found in nests of *V. germanica* and *V. pensylvanica*) (MacDonald et al., *1980*); however, *V. flavopilosa* carton is noticeably sturdier, and cell size is significantly larger than that found in *V. maculifrons* and *V. vulgaris* nests. Accordingly, workers and queens of the new species are larger and similar to *V. germanica* and *V. pensylvanica* in this respect. At least in the southeast, colony seasonal cycle is shorter, ending a month or so earlier than that of *V. maculifrons*; thus, colony size was noticeably smaller. Typical *V. flavopilosa* colonies in western North Carolina completed their cycle by early October, during which time a peak worker population of 500 to 1,000 constructed from 2,000 to 5,000 cells consisting of nearly 20 percent queen cells; therefore, nests of *V. flavopilosa* collected in late summer contained 2,500 to 4,000 fewer worker cells than those of *V. maculifrons* collected at the same time and locality (table 8).

Since *V. flavopilosa* was only recently described as a species, no studies of behavior or nest associates are in the literature.

For the same reason, the pest status of *V. flavopilosa* is unevaluated; however, since workers are scavengers, *V. flavopilosa* probably presents a pest problem similar to that of other *V. vulgaris* group species. Queens of this species establish nests along roadsides and in yards. Three *V. flavopilosa* nests in structures have been found in New York (R. Keyel, Cornell Univ., personal commun.). Based on a small collection from Minnesota, *V. flavopilosa* workers are attracted to heptyl butyrate to some degree; response to protein baits is unevaluated.

Vespula germanica.—Native to Europe, *Vespula germanica* (German yellowjacket) has been introduced into New Zealand (Thomas, *1960*), Tasmania (Spradbery, *1973b*), South Africa (Whitehead and Prins, *1975*), Chile (Peña et al., *1975*), Sydney, Australia (R. Edwards, Rentokil Ltd., Sussex, England, personal commun.) and the United States (Menke and Snelling, *1975*). The known distribution of this species in North America, as of 1977, is given in figure 57.

In Europe, *V. germanica* nests are usually subterranean, but they may be aerial or in roofs, attics, and between the walls of houses (Spradbery, *1973a*). In North America, nearly all reported nests have been in structures. Eighteen of 22 colonies studied in Tompkins County, New York, during 1977, built nests between the walls of buildings (R. Keyel, Cornell Univ., personal commun.). Colonies are usually annual, but perennial colonies are not infrequent in New Zealand (Thomas, *1960*) and Tasmania (Spradbery, *1973b*).

Spradbery (*1973a*) discussed the huge nests constructed by perennial colonies of *V. germanica* in New Zealand (Thomas, *1960*) and Tasmania. In New Zealand, one aerial nest was 14 ft 11 inches by 5 ft by 2 ft, and a subterranean nest (47 by 40 by 38 inches) with 27 combs weighed about 100 lb. A subterranean nest in Tasmania measured 6 by 2.5 by 4 ft, had 30 combs, and was comprised of 1.5 million cells. From these data, it was estimated that the largest New Zealand nest had 3 to 4 million cells and weighed 1,000 lb.

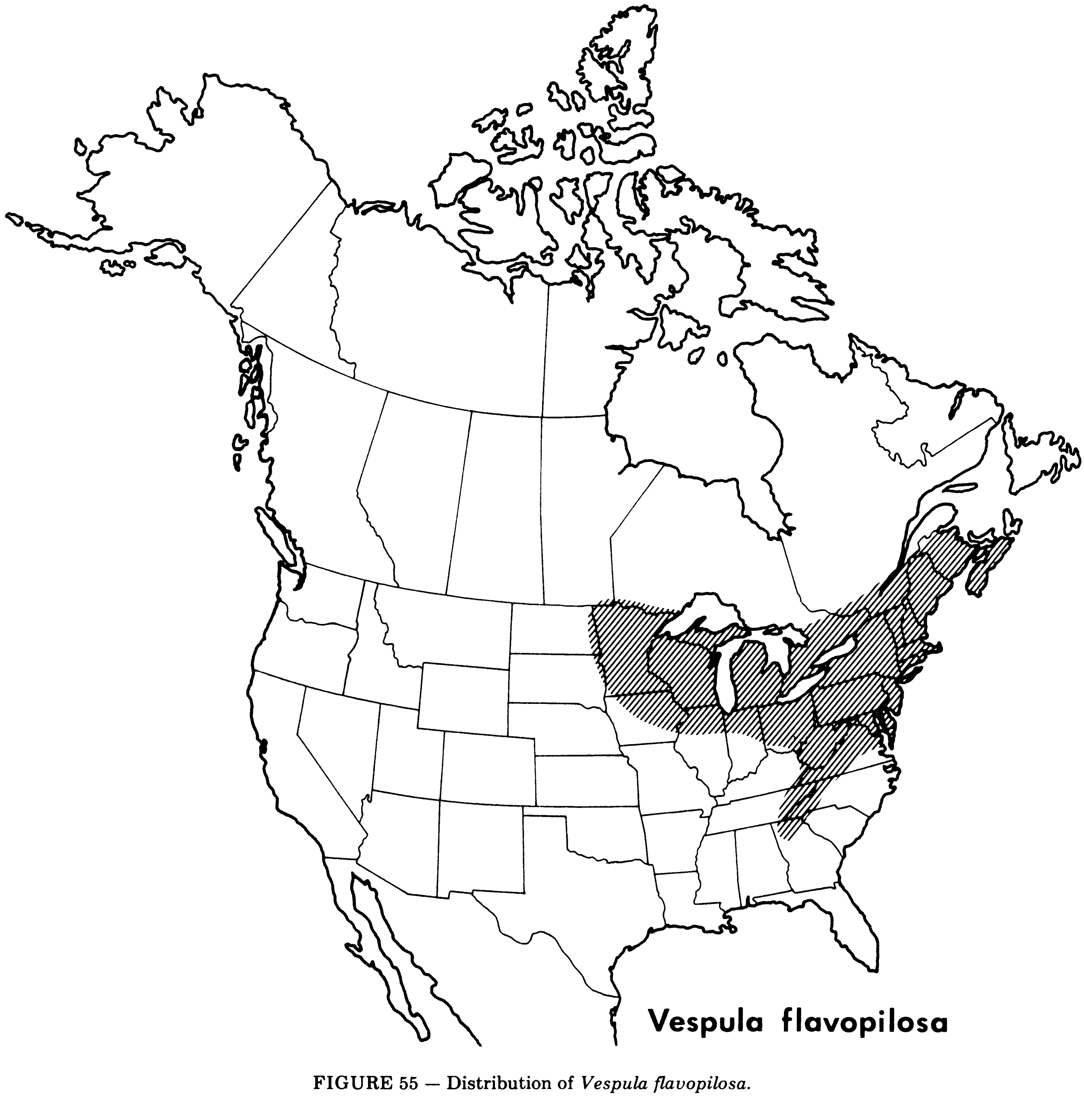
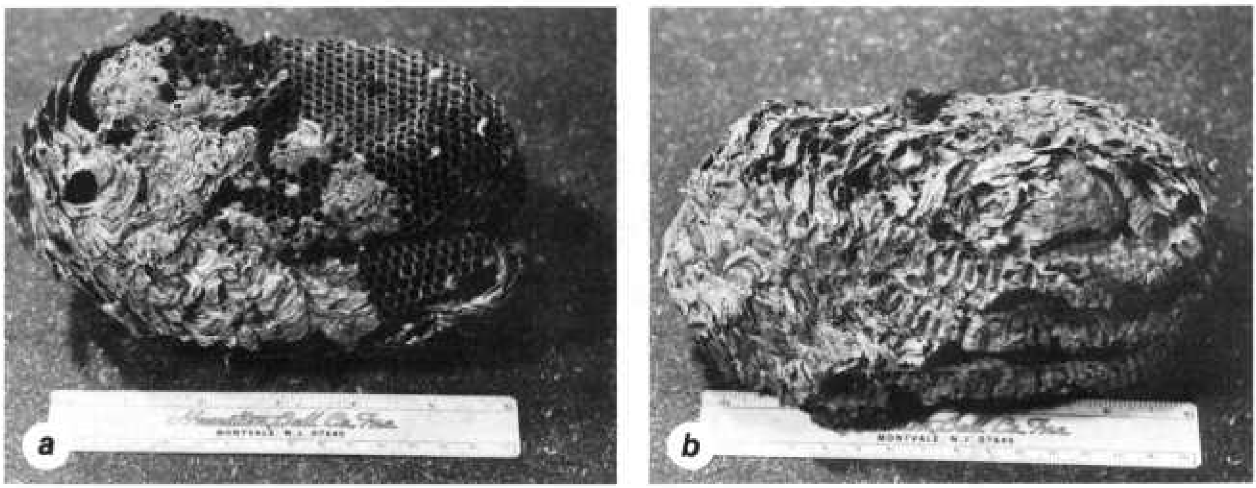


FIGURE 55 — Distribution of *Vespula flavopilosa*.



PN-6541

FIGURE 56 — *Vespula flavopilosa* mature nest, New York: *a*, Bottom view; *b*, top view (R. Keyel).

TABLE 8.—Vespula flavopilosa *and* V. maculifrons *colonies collected during 1974 in northwestern Georgia and southwestern North Carolina (MacDonald et al.,* 1980)[1]

Species	Colonies	Worker cells in nest: Largest	Worker cells in nest: $\overline{X}$	Worker combs	Maximum workers
	- - - - - - *Number*	- - - - - -			
V. flavopilosa	23	3,844	1,871 (N = 19)	3.2	1,332
V. maculifrons	32	9,700	4,422 (N = 14)	4.8	4,839
			[2]6,211 (N = 7)	5.3	——

[1]Since most colonies were sampled early in the period of queen-cell construction, only comparisons of worker cells and worker cell combs were made.

[2]*V. maculifrons* colonies in which queen cell construction had begun.

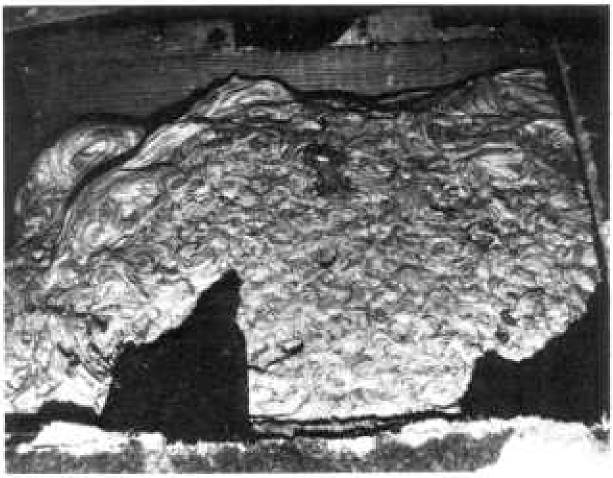
Typical nests are considerably smaller and are similar in size to nests of *V. pensylvanica.* Spradbery (*1973a*) described a colony collected in early September in Great Britain, which was comprised of 1,820 workers, 447 males, 147 new queens, and the foundress. The nest had 8 combs with a total of 6,341 cells, including 1,214 queen cells, Nests built by mature colonies in Israel have 1 to 15 combs (Ishay and Brown, *1975*).

Very little data are available on *V. germanica* colonies in North America, although pest control operators report large nests are not uncommon in the Washington, D.C., area. One located within the framework of a house porch and examined in late August contained 11,540 cells in seven combs (fig. 58). Another, situated in an attic, measured nearly 80 cm in diameter by 80 cm long (J. Nixon, Silver Spring, Md., personal commun.) (fig. 59). The nest was comprised of only six combs. The large size was mostly due to multiple envelope layers, probably a response to high temperatures in the attic. As reported from New York and Ohio (Morse et al., *1977*), colonies in the mid-Atlantic States may be active well into December.

FIGURE 57 — Distribution of *Vespula germanica.*

The most significant work on the behavior of *V. germanica* is that of Montagner (*1966*) who reported a dominance hierarchy among workers. More dominant workers solicit and receive food from foragers, but dominance is not correlated to ovarian development. Other works on *V. germanica* behavior include studies on foraging (Free, *1970*), worker behavior (Archer, *1972b*), sounds produced by larvae (Ishay and Brown, *1975*), and nest usurpation (Nixon, *1935*).

V. germanica workers accept a wide variety of arthropods as prey and are opportunistic in the exploitation of food sources. Most workers forage within several hundred meters of the nest, but some will travel up to 1,200 m (Ferro, *1976*). They are also notorious scavengers for



PN-6542
FIGURE 58 — *Vespula germanica* nest, Washington, D.C., area (J. Nixon).

protein and are attracted in great numbers to sweets.

V. germanica is a problem to beekeepers (Walton and Reid, *1976*), a general nuisance in bakeries, markets, parks, and butcher shops (Kemper and Döhring, *1967*), and, in New Zealand, has been responsible for the closing of several schools because of the great number of nesting colonies in surrounding playgrounds. However, they are also beneficial as a great number of adult flies of wool maggots (blow flies, Calliphoridae; Thomas, *1960*) and muscid flies (Schmidtmann, *1977*) are taken as prey.

This species has become more abundant and seems to be replacing *V. maculifrons* as the most abundant pest yellowjacket in some areas of the East (Morse et al., *1977*). As it becomes more firmly established, it has spread slowly westwards and reached Indiana as of 1976. Indeed, five colonies were located in houses in Lafayette, Ind., during the late summer and fall of 1977. None could be removed for sampling as they were deep in hollow walls or flooring. During the summer of 1978, several colonies of *V. germanica* were located on the campus of Michigan State University. Subsequently, this species was found distributed throughout much of the State and was responsible for many of the reported yellowjacket problems. Obviously, the known distribution of this species is rapidly expanding.

Vespula maculifrons.— *Vespula maculifrons* (eastern yellowjacket) is widespread in the Austral Region of North America from southern Manitoba to Montana and New Mexico and from there across to the eastern seaboard (fig. 60). Biological investigations of this species were conducted by Balduf (*1968a, 1968b*), Haviland (*1962*), MacDonald and Matthews (*198_a)*, Preiss,[4] and Shew.[5]

[4]Preiss, F.J. Nest site selection, microenvironment and predation of yellowjacket wasps, *Vespula maculifrons* (Buysson), (Hymenoptera: Vespidae) in a deciduous Delaware woodlot. M.S. thesis, University of Delaware. Newark. 81 pp. 1967. [Mimeographed.]

[5]Shew, R.L. The biology and control of vespine wasps. M.S. thesis, Ohio State University. 59 pp. 1966. [Mimeographed.]

PN-6543
FIGURE 59 — *Vespula germanica* nest in attic of house, Washington, D.C., area (J. Nixon).

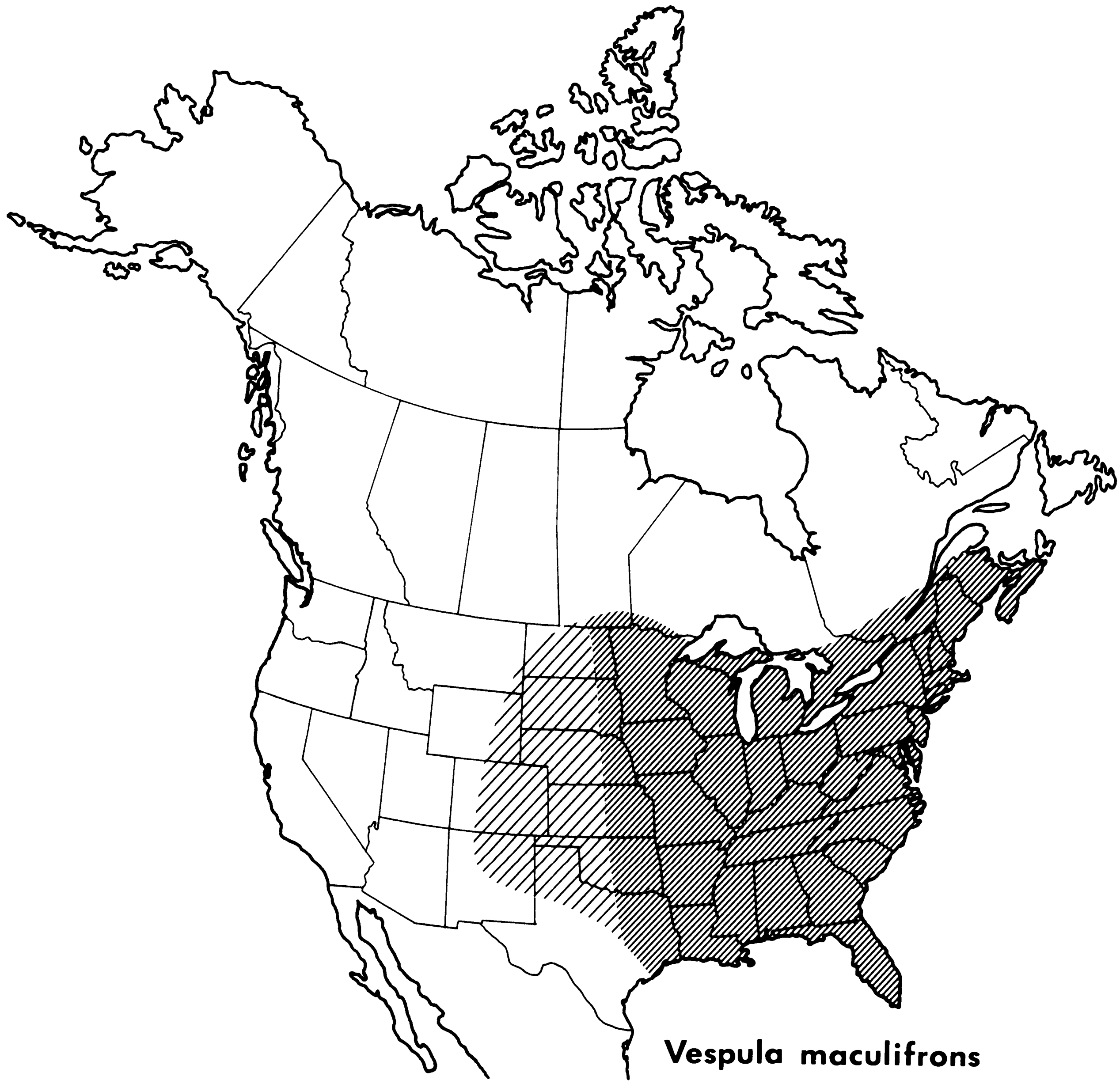


FIGURE 60 — **Distribution of *Vespula maculifrons*. Lighter pattern indicates scattered occurrence.**

V. maculifrons typically builds its nests (fig. 61) in subterranean locations in yards, along roadsides and creek banks, in hardwood forests, and in urban environments. MacDonald and Matthews (*198_a*) reported 143 of 145 nests in the southeast were subterranean and commonly found in creek banks in hardwood forests. Subterranean nest locations were also reported by Haviland *(1962)*, Preiss,[6] and Shew.[7] Other nest locations have also been described such as in decaying stumps (Green et al., *1970* and Shew[8]),

[6]See footnote 4.

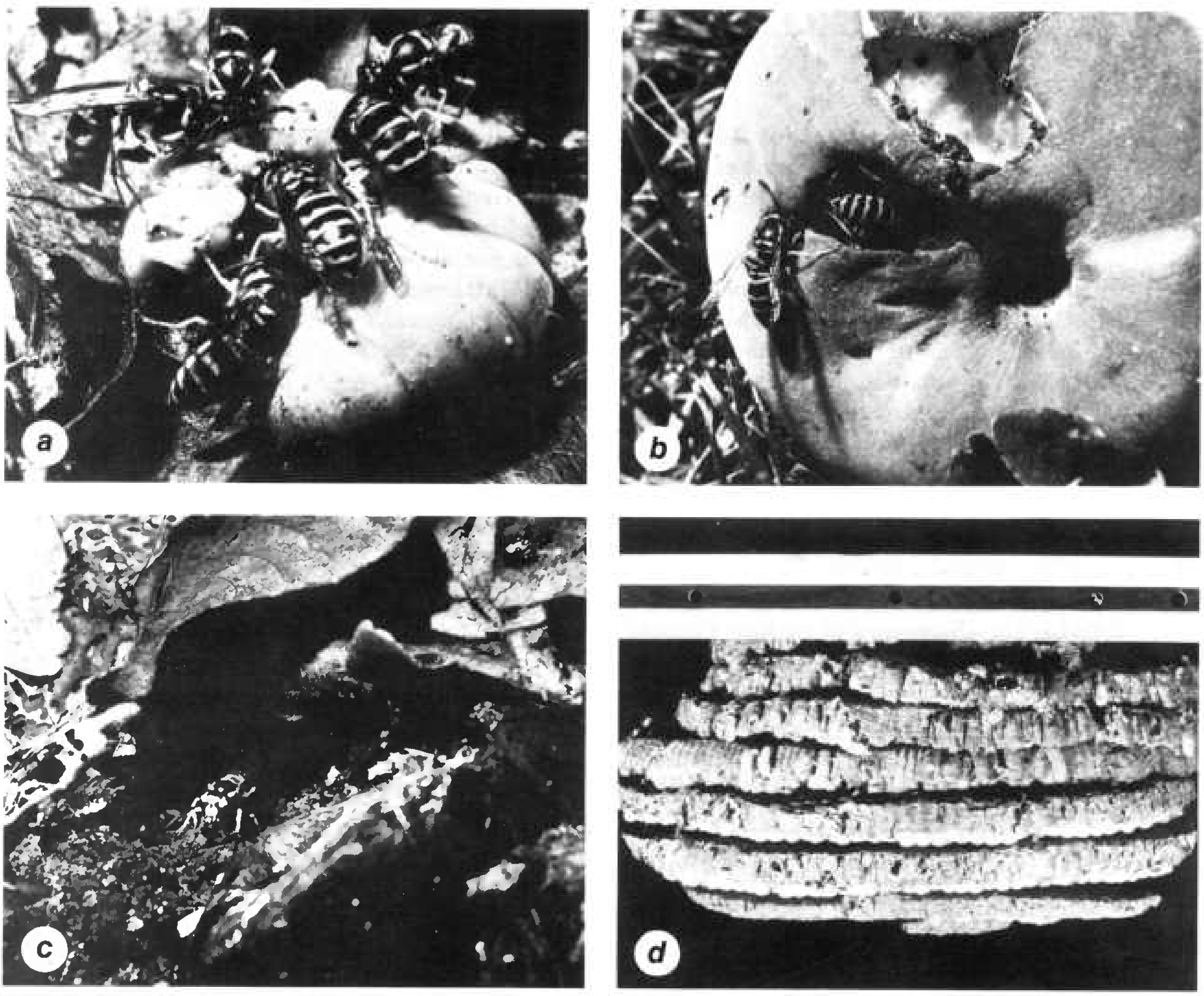
[7]See footnote 5.

[8]See footnote 5.

attics (Balduf, *1968a*, *1968b*; MacDonald and Matthews, *198_a*; Simon and Benton, *1968*), in the walls of structures (Balduf, *1968b*, Green et al., *1970*), and even in abandoned cars and inside the hull of a boat. In the Washington, D.C., area, nests in walls now constitute nearly half of homeowner complaints regarding *V. maculifrons* (J. Nixon, Silver Spring, Md., personal commun.). This species also frequently nests in structures in Indiana.

Colonies in Georgia have a very long seasonal cycle. Reproductive production does not begin until late September but continues well into December. In the North, colonies are initiated in May or June and usually peak in the latter part of August or September. The seasonal cycle is somewhat shorter than in the South, and colonies typically are smaller.

Haviland (*1962*) collected 10 nests that ranged from 9.5 to 30 cm in diameter (table 9). The envelope of these nests was tan-brown and very fragile. The largest had eight comb levels and contained 2,800 adults. Simon and Benton (*1968*) observed, and later collected on December 5 in Pennsylvania, a nest from the loft of a barn that contained 10,960 cells, including 880 queen cells. The adult population of the colony was 5,062 (598 queens, 3,255 males, and 1,209 workers). A large colony of *V. maculifrons* in the southeast typically consists of 3,000 to 5,000 workers at



PN–6544

FIGURE 61 — *Vespula maculifrons*: *a*, Workers attacking a grub; *b*, workers feeding on a fallen peach; *c*, worker in nest entrance with a load of soil, subterranean colony in a Delaware woodlot (*a–c*, W.D. Lord); *d*, combs of a nest indicating size.

TABLE 9.—*Analysis of 10 nests of* Vespula maculifrons *from Washington, D.C. (Modified from Haviland,* 1962)

Nest No.	Date examined	Combs	Adults: Fall queens	Adults: Males	Adults: Workers	Total cells	Queen cells
		Number					
1	6-27-53	4	0	0	127	1,101	0
2	7-07-56	4	0	0	126	1,495	0
3	7-30-50	5	0	0	390	2,344	0
4	8-08-56	2	0	0	590	2,836	0
5	8-12-56	5	0	0	635	2,665	0
6	9-15-50	5	1	30	1,026	2,967	424 (14 percent)
7	9-16-60	6	120	1,023	1,281	9,762	866 (9 percent)
8	9-27-61	5	54	414	764	4,538	158 (3 percent)
9	9-28-60	8	43	654	2,192	7,755	681 (9 percent)
10	10-26-54	4	12	5	7	1,683	76 (5 percent)

its peak and constructs a nest of 10,000 to 15,000 cells of which nearly 30 percent are queen cells (MacDonald and Matthews, *198_a*; table 10 of this handbook).

Virtually every mature *V. maculifrons* colony in Georgia and North Carolina harbored large numbers of scavenger fly larvae in the soil beneath the nest. Larvae of *Dendrophaonia querceti* were by far the predominant associate, and *Fannia* larvae were present in lower numbers in nearly every nest cavity. Larvae of *Triphleba lugubris* were rarely encountered, but when present in nearly abandoned nests they totally invaded the nest proper. Only 3 of 145 nests were infested with *Sphecophaga vesparum burra*, and then only a few cells were parasitized.

In Georgia and western North Carolina, *V. maculifrons* is the primary host of the facultative social parasite, *V. squamosa* (MacDonald and Matthews, *1975*). An estimated 40 percent of the *V. maculifrons* colonies in this area are usurped by queens of the parasite (MacDonald and Matthews, *198_b*).

There are isolated behavioral observations on *V. maculifrons* (Balduf, *1968a*; Beamer, *1925*; Simon and Benton, *1968*), but no studies on foraging behavior or interactions within the nest.

TABLE 10.—***Summary of mature*** **Vespula maculifrons** ***colonies collected after October 15, 1974-75 in and around Athens, Ga. (MacDonald and Matthews,*** 198_ a)

Parameter	1974		1975	
Colonies located	30		55	
	Largest	Average	Largest	Average
Total cells per nest	11,407	6,461 (N = 12)	14,105	9,196 (N = 10)
	Average	Percent of total cells	Average	Percent of total cells
Queen cells per nest	1,622 (N = 12)	25 percent	2,780 (N = 10)	30 percent
Maximum workers per colony	4,875			
Combs per nest	Average		[1] Average	
Worker	3.9		4.8	
Mixed	0.9		0.5	
Queen	2.8		3.6	
Total	7.7		8.9	

[1] Due to late-season collecting, a large colony was not sampled at its peak.

Although *V. maculifrons* workers prey upon economically important insects, such as earwigs (Kurczewski, *1968*) and fall webworm larvae (Morris, *1972*), this aspect of their biology usually has been ignored. In most areas in which it occurs, *V. maculifrons* is the primary pest yellowjacket because of its scavenging habits and the great number of colonies that build nests in yards, golf courses, recreational areas, and buildings. In some areas of the northeast, it appears that *V. maculifrons* is being replaced by *V. germanica* as the primary pest species, and in the southeast *V. squamosa* competes with *V. maculifrons* for primary pest status.

Vespula pensylvanica.—*Vespula pensylvanica* (western yellowjacket) occurs in the Canadian and Transition Zones in western North America. This species also occurs in Hawaii on the islands of Kauai (Williams, *1927*), Oahu (Williams, *1937*), Maui, and Hawaii (J. W. Beardsley, Univ. Hawaii at Manoa, personal commun.), and in Mexico (Ebeling, *1975*; Snelling, *1970*). Distribution is given in figure 62.

Nests of *V. pensylvanica* are usually subterranean (Bohart and Bechtel, *1957*; Duncan, *1939*; Smith, *1956*), and most are constructed in rodent burrows (MacDonald et al., *1974*). A few nests are built in other dark cavities such as in attics or between the walls of houses (Buckell and Spencer, *1950*; Ebeling, *1975*; Spencer, *1960*). In Pullman, Wash., subterranean nests were typically 10 to 15 cm below the soil surface (fig. 63 *d*, *e*) with entrance tunnels of 10 to 30 cm (MacDonald et al., *1974*).

Duncan (*1939*) tabulated one colony of *V. pensylvanica* comprised of 4,768 workers and the foundress queen. The colony probably would have grown for another month if it had not been collected, but it had already constructed a nest of 10,468 cells. He mentioned another nest of 17.25 by 16 by 10 inches but gave no other data. Table 11 lists the size of mature (producing queens) colonies collected 1971-77 in Pullman, Wash., and La Grande, Oreg. The largest nest collected contained 12,316 cells, and the maximum number of workers in a colony was 3,933. Most colonies had nests of 4,000 to 10,000 cells.

MacDonald et al. (*1975b*) discussed nest associates occurring with *V. pensylvanica* and *V. atropilosa*. As a rule, at least until colony decline, *V. pensylvanica* has cleaner nests and fewer associates than *V. atropilosa*. In addition, the ichneumonid parasite, *Sphecophaga vesparum burra*, was found in a *V. pensylvanica* nest for the first time in southeastern Washington in 1977. The nest contained one adult parasite, one empty cocoon, and four intact cocoons; thus, only one of the 186 analyzed nests from 1971-77 contained this parasite. This may be due to the behavior of *V. pensylvanica* workers, which immediately attack and kill introduced *Sphecophaga*, whereas *V. atropilosa* workers frequently ignore adult *Sphecophaga* when they are introduced.

V. pensylvanica workers will accept a wide variety of prey (Akre et al., *1976*; MacDonald et al., *1974*). Included are slugs, phalangids, spiders, grasshoppers, flies, cercopids, and bugs. The preponderance of prey collected were members of Hemiptera-Homoptera. Members of this species also scavenge extensively for protein, especially later in the year.

The behavior of *V. pensylvanica* colony members in the nest was observed by Akre et al. (*1976*). The division of labor among workers is not as sharply defined as in honey bees, and workers performed a number of activities during the same day. Social interactions similar to the dominance hierarchy described by Montagner (*1966*) for *V. germanica* and *V. vulgaris* were exhibited by the workers of *V. pensylvanica*. In another study (Akre et al., *1975*), 80 percent of the workers foraged within 1,100 ft of the nest.

V. pensylvanica is the primary pest yellowjacket in the West from Washington to California. Periodic population outbreaks, associated with warm, dry springs, occur every 3 to 5 years or slightly longer, which create severe problems for people engaged in logging, raising fruit, or in recreation-associated activities. A number of colonies establish their nest in yards or recreation areas, and the chance of colony disturbance resulting in stings is great. Since this species is a scavenger, it is a constant companion at picnics or at food dispensing facilities and frequently must be controlled.

Vespula vulgaris.—*Vespula vulgaris* (common yellowjacket) is a Holarctic species transcontinentally distributed in the Nearctic Region (fig. 64). In western North America, this species is prevalent in heavily forested areas. In Hawaii, *V. vulgaris* occurs only on the island of Maui (Ho-

TABLE 11.—*Size of mature (producing queens)* Vespula pensylvanica *colonies 1971-77*[1]

Year	Nests	Most combs	Fewest combs	Average number of combs	Fewest cells	Most cells	Average number of cells	Maximum workers	Total analyzed nests
					Number				
1971	3	8	4	6.0	8,595	12,316	10,751	2,266	6
1972	6	8	5	6.3	1,422	8,013	4,116	1,125	9
1973	28	7	4	5.9	2.547	6,689	4,623	1,151	47
1974	16	8	6	7.0	2,926	10,438	6,051	1,883	31
1975	13	7	4	6.1	1,342	6,760	3,859	1,777	55
1976[2]	0	7	3	5.0	703	4,919	2,494	924	11
1977	18	9	4	6.3	1,574	11,838	6,842	3,933	30
1971-77[3]	84	9	4	6.3	1,342	12,316	5,435	3,933	178

[1]Colonies from 1971-74 are only from Pullman, Wash.; colonies were also collected from La Grande, Oreg., during 1975-77.

[2]Due to late season, no mature colonies were collected. Totals include all nests.

[3]**Excluding 1976.**

warth, *1975*). It also occurs in Mexico (Ebeling, *1975*). Detailed biological studies of this species, such as those of Archer (*1972a, b, c, 1973, 1977b*), Guiglia (*1972*), Kemper (*1961*), Kemper and Döhring (*1967*), and Potter[9], were done in Europe. These data and much of his own have been summarized by Spradbery (*1973a*). No in-depth biological study of this species in America is available, but Balduf (*1968b*) made some observations on nests and seasonal development of colonies in Minnesota.

In Europe, most *V. vulgaris* nests are subterranean, although some nests are constructed in the walls of houses or even in aerial locations (Spradbery, *1973a*; Weyrauch, *1935*). In the Western United States, this species usually builds its nests in rotten logs or stumps, in forest duff, or in the soil (fig. 65). Entrance tunnels to nests vary from 4 to 100 cm, usually 10 to 15 cm, with most nests found about 10 cm below the soil surface. Some colonies, especially in western Washington, construct nests between the walls of houses. Similarly, in New York, 11 of 21 nests located during 1977 were between the walls of a building (R. Keyel, Cornell Univ., personal commun.). The nest envelope and combs are usually constructed of decayed wood fibers and are red- to tan-brown and very brittle.

In England, the nest is initiated in May and ultimately contains an average of nine combs when the colony peaks development in September (Spradbery, *1973a*). In Washington, northern Idaho, and northeastern Oregon, the nest is also initiated in May or early June, and colonies peak in September. Some colonies are still active in October, but rarely in November; however, nests are comprised of only three to five combs.

The maximum number of cells in a nest analyzed by Spradbery (*1973a*) was 16,832 including 3,888 queen cells. In Germany, Kemper (*1961*) reported a nest with 21,692 cells, including 4,028 queen cells. Duncan (*1939*) illustrated one large nest of *V. vulgaris* in California constructed by a perennial colony that had 22 functional queens at the time of collection. The nest had 21 comb levels, and was 46 by 40 by 30 inches. No count was made of the adult population but they filled four 1-gallon jars. Four gallons of *V. pensylvanica*, a larger species, would be over 60,000 workers. Another California colony contained 2,951 workers when killed. Analyses of 19 mature nests collected during 1975-77 in Washington, Idaho, and Oregon showed them to be much smaller, averaging 2,100 cells, with 10 percent reproductive cells. The largest nest

[9]Potter, N. B. A study of the biology of the common wasp, *Vespula vulgaris* L., with special reference to the foraging behavior. Ph.D. thesis, Univ. Bristol, England. 75 pp. 1964. [Mimeographed.]

contained 4,972 cells. No study has been made of the nest associates of *V. vulgaris* in North America; however, 7 of the 19 nests mentioned above contained cocoons of the pupal parasite, *Sphecophaga vesparum burra*.

Behavioral interactions inside the nest were studied by Montagner (*1966*) and Potter.[10] Potter's studies included foraging behavior and daily

[10]See footnote 9.

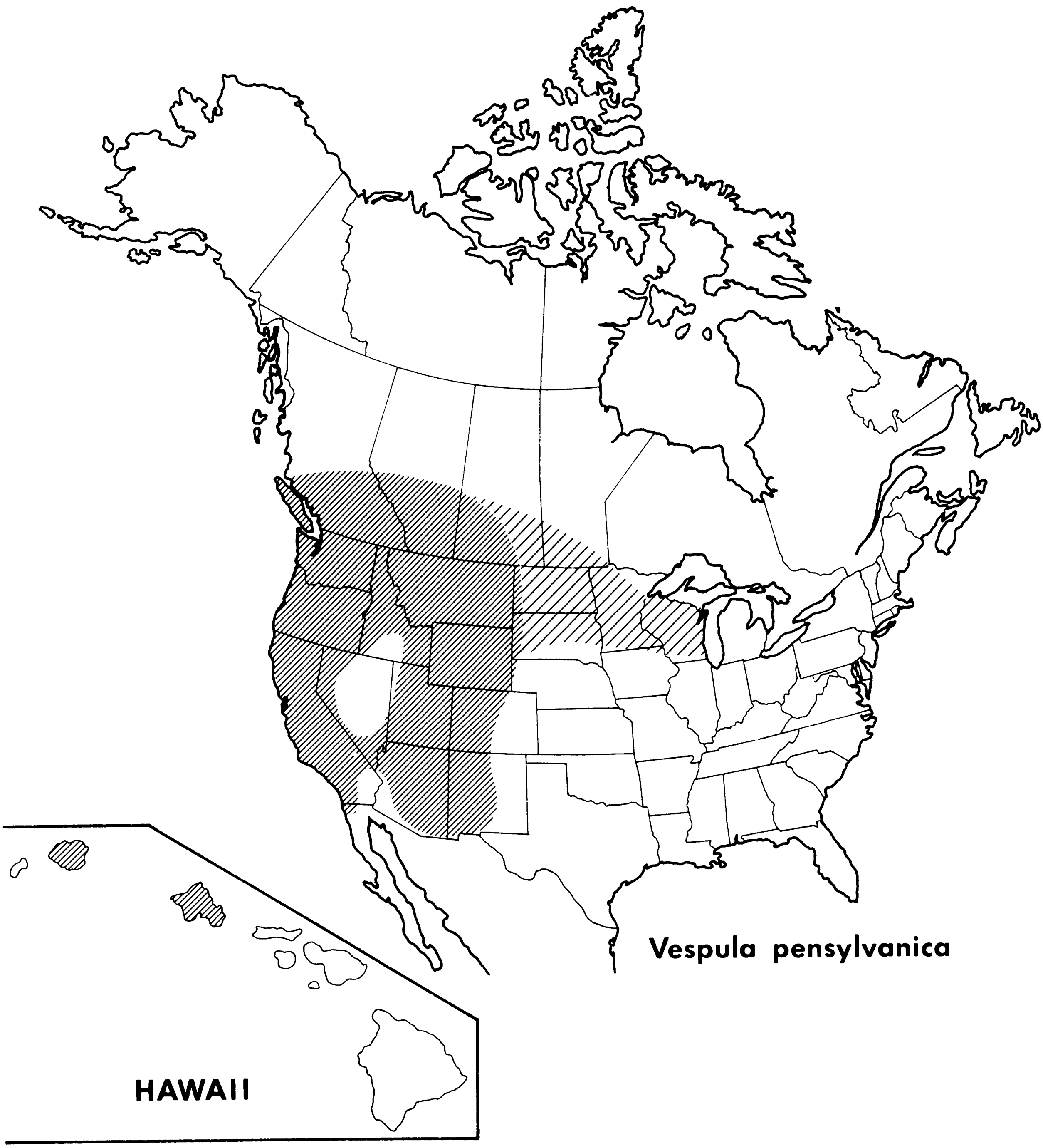
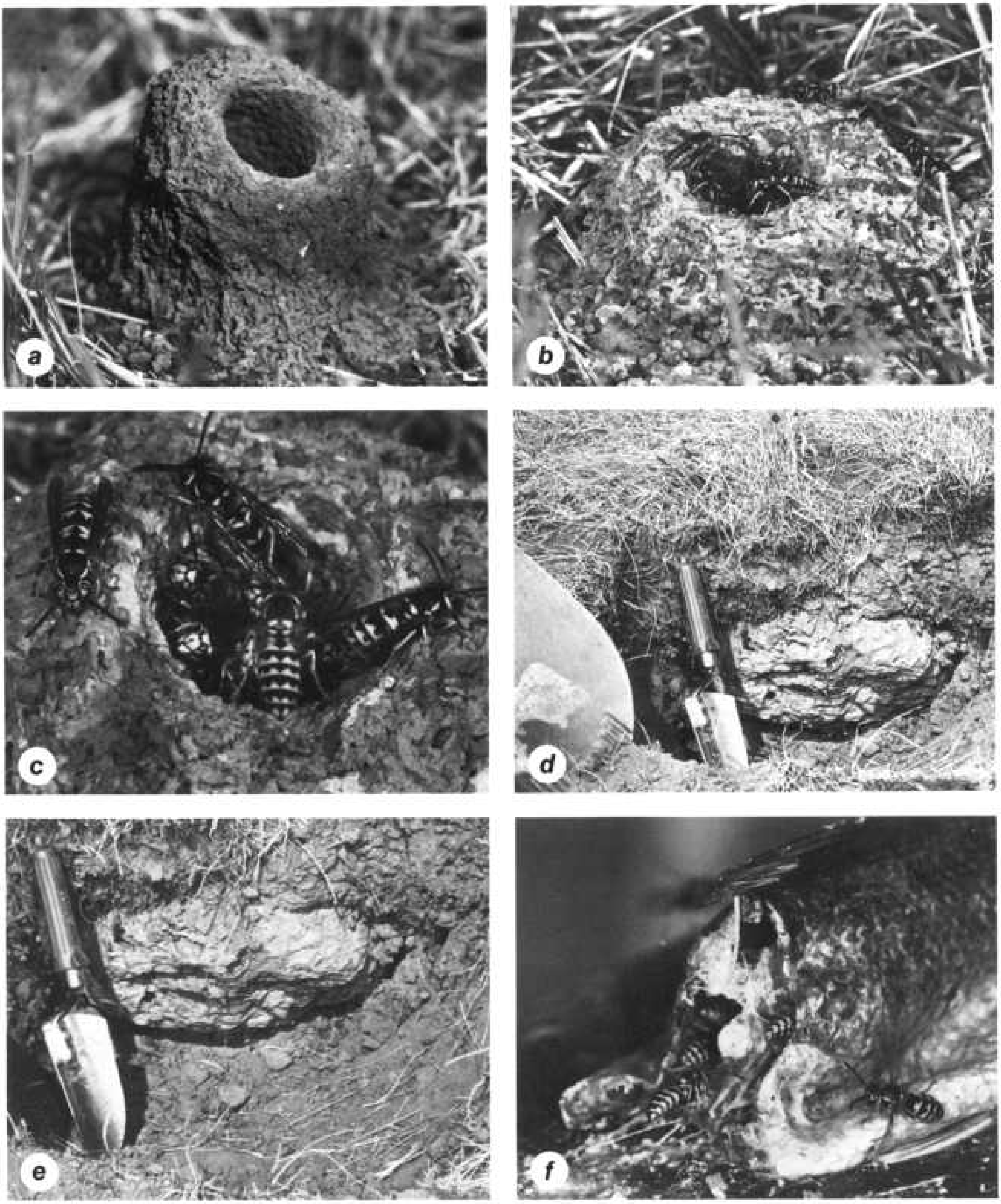


FIGURE 62 — Distribution of *Vespula pensylvanica*. Lighter pattern indicates scattered occurrence.



PN–6545

FIGURE 63 — *Vespula pensylvanica*: *a*, Mud turret surrounding nest entrance late in the season; *b*, *c*, workers entering and leaving, guard workers; *d*, *e*, subterranean nest near Washington State University golf course; *f*, workers scavenging flesh from fish carcass.

activities of the members of the colony, whereas Montagner studied social dominance (hierarchy) among the workers of the colony with certain individuals being dominant and demanding food from foragers.

V. vulgaris workers are predators on a wide variety of prey, similar to that attacked by *V. pensylvanica*, including a variety of caterpillars, small beetle larvae, hemipterans, homopterans, and flies. In addition, workers of this species are notorious scavengers attracted to nearly any protein or sugar source.

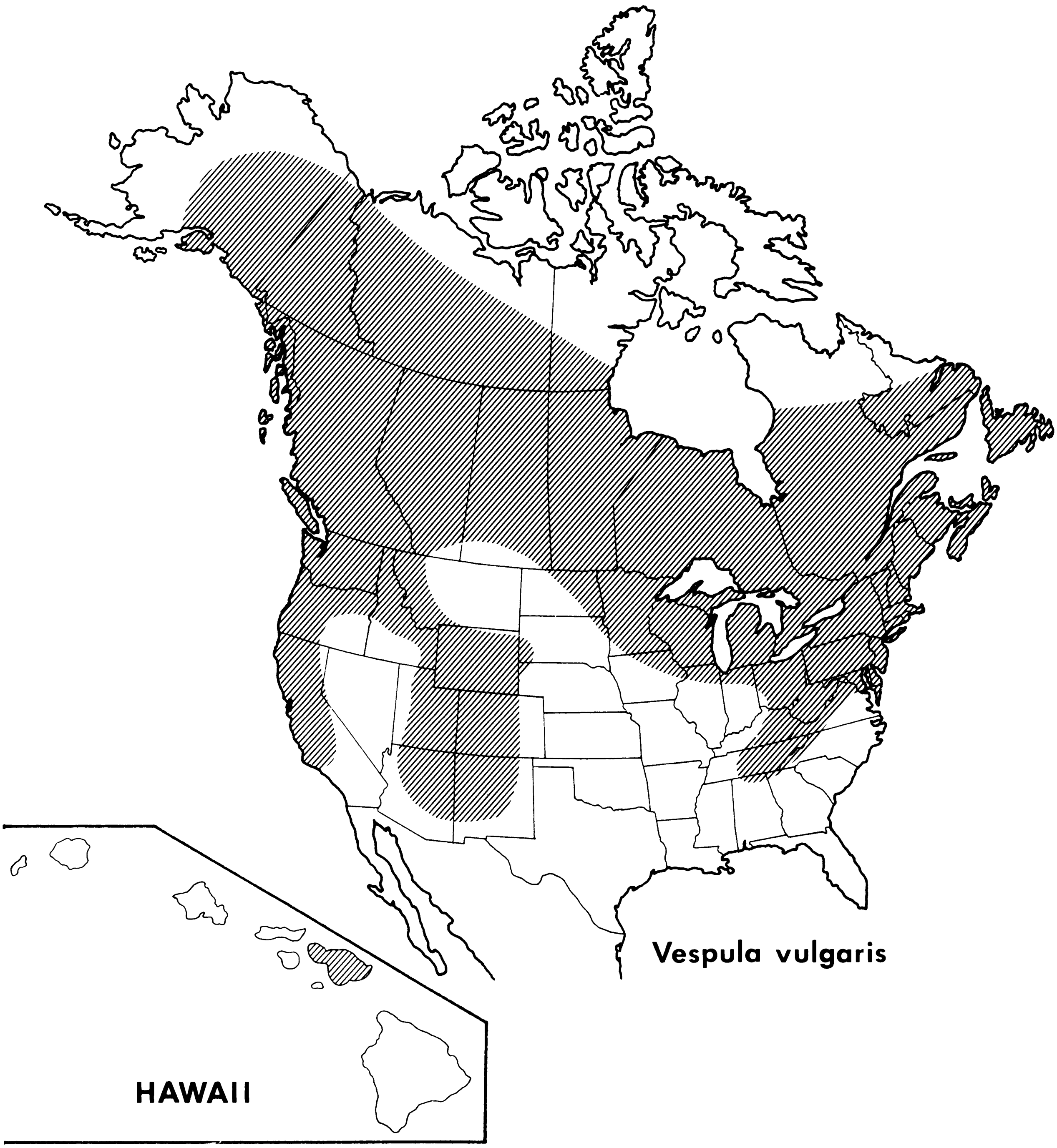


FIGURE 64 — Distribution of *Vespula vulgaris*.

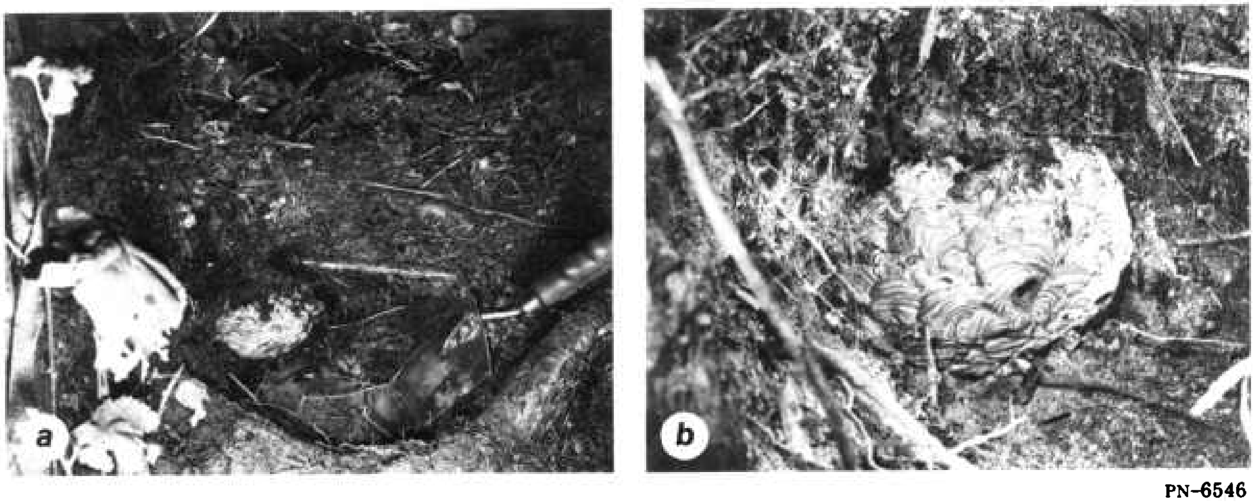


FIGURE 65 — *a, b*, Subterranean *Vespula vulgaris* nests, Harrison, Idaho.

This species is a nuisance in food-dispensing facilities in Germany (Kemper and Döhring, *1967*), is described as being the most annoying to humans of any yellowjacket in Norway (Løken, *1964*), and is second only to *V. pensylvanica* as a pest species in western North America (Ebeling, *1975*). In San Mateo County, Calif., these yellowjackets are the subject of control programs nearly ever year (Grant et al., *1968*). The 1973 outbreak of yellowjackets in the Pacific Northwest included high populations of *V. vulgaris* in forested areas such as western Washington and northern Idaho. In 1974, severe problems were caused by high populations of this species in Alaska (Davis, *1978*).

ECONOMIC IMPORTANCE

It is impossible to accurately assess the true economic importance of yellowjackets in North America because information pertaining to the beneficial aspects of these wasps remains largely unreported, and even the pest status of several species is not fully documented. For example, although researchers have frequently observed yellowjackets preying on defoliators in forests, little has been published about this predation and its possible values. Similarly, no data are available on the beneficial nature of yellowjackets in other situations, such as in agriculture or urban environments. Conversely, the pestiferous nature of scavenger species has been only sporadically and incompletely reported with no comprehensive evaluation of possible economic impact.

Beneficial Aspect

Reports mentioning the beneficial aspect of yellowjackets include those by Gaul (*1952*), Greene et al. (*1976*), Kuhlhorn (*1961*), MacDonald et al. (*1974*), and Schmidtmann (*1977*). These studies showed that yellowjackets readily attacked house flies and blow flies. From these data, and from observations of yellowjacket workers preying on flies in large concentrations in places like mink and cattle ranches, it can be inferred that yellowjackets help to control fly populations. Other economically important insects used by yellowjackets as prey are *Lygus* bugs, several species of Homoptera including spittle bugs, various caterpillars, and grasshoppers (MacDonald et al., *1974*). Fall webworm larvae, *Hyphantria cunea* Drury, are taken as prey by *Vespula maculifrons*, *V. vulgaris*, and *Dolichovespula arenaria* (Morris, *1972*). White et al. (*1969*) and Howell and Davis (*1972*) showed *V. pensylvanica*, and perhaps workers of other species of yellowjackets, attacked codling moths, *Laspeyresia pomonella* (L.), within their experimental plots and interfered with their test results. In addition, R. W. Zwick (Oreg. State Univ., personal commun.) showed that workers of *D. arenaria* could completely control pear psylla on pear under caged conditions. The above reports imply that yellowjackets are beneficial and help control populations of a number of insect pests. Still needed are studies on yellowjacket predation that show where it is of possible benefit to man and his crops. We believe that many species will be found to be highly beneficial once data are collected.

Economic Losses

Although most yellowjackets can be regarded as beneficial, a few pestiferous species are responsible for economic losses (which can be considerable) in agricultural, recreational, and urban-suburban environments during years of peak populations or outbreaks. Again, there is a lack of information as to the economic losses which can be attributed directly to the activities of yellowjackets. Most information on this subject is found in vague, fragmentary reports, which, at best, are only attempts to estimate losses in a particular locality. For example, Poinar and Ennik (*1972*) cited a report by Hawthorne,[11] stating that 1968 losses to agricultural operations in California were estimated at $200,000. These losses were attributed to disruptions due to *Vespula* spp. bothering and stinging pickers, feedlot workers, laborers at meat processing plants, and other persons involved in agriculturally oriented occupations.

A brief description of some of the many problems attributed to yellowjackets follows. Information was gathered from accumulated newspaper and magazine articles, journals, technical bulletins, personal communications from other researchers, and letters from numerous citizens throughout North America who have had yellowjacket problems.

[11]Hawthorne, R. M. Estimated damage and crop loss caused by insect/mite pests. 1968. Calif. Dept. Agric. Bur. Ent., 11 pp. 1969. [Mimeographed.]

Losses in Agricultural Areas

Yellowjackets often become serious pests in fruit-growing regions, and during years of abundance they may stop harvesting operations. This occurred at a peach orchard in Oregon in 1969 when thousands of *Vespula pensylvanica* workers were attracted to the fruit. Pickers were frequently stung as they moved their ladders over yellowjackets feeding on the soft, windfallen fruit on the ground. Losses due to harvesting delays affect orchard workers in lost wages and in medical expenses that may be incurred. The grower must pay higher production costs, and additional losses result from lowered income from reductions in fruit quality.

Yellowjackets have also been troublesome to growers in pear and apple orchards (Buckell and Spencer, *1950*; R. W. Zwick, Oreg. State Univ., personal commun.). The problem occurs during years of peak populations of the aerial-nesting species *Dolichovespula arenaria* (aerial yellowjacket) and *D. maculata* (baldfaced "hornet") since many colonies build their nests in the fruit trees. Laborers are commonly stung as they perform routine chores in the orchard that disturb and redisturb the colonies.

Similar problems also occurred from thousands of foraging *Vespula* and *Dolichovespula* spp. workers attracted to a fruit processing plant in Toppenish, Wash., during August and September 1975. Most yellowjacket colonies had entered decline, and the workers were attracted by the many sweet juices and fruit remnants scattered throughout the plant. Some laborers were stung, but more importantly, many were terrified of the yellowjackets and production declined greatly. Changes were made in the plant operations so that less food debris and juices were available to attract yellowjackets, and other control procedures were employed before the problem was alleviated.

Duncan (*1939*) and Howell (*1973*) reported yellowjackets feeding on grapes and removing the juices. This appears to be especially true in recent years in newly developed vineyards of wine grapes in the Pacific Northwest. For example, several growers in Oregon and Washington reported losses of nearly half their crop of red grape varieties (mostly pinot noir) during 1975 due to yellowjackets. Specimens examined from one vineyard were *V. pensylvanica*, but other species might also be involved. According to the growers, the yellowjackets land on the larger clusters, sever the skin of one or more grapes and feed on the juice. They reported that many clusters were damaged and, perhaps equally important, the remaining grapes are susceptible to the brown or bunch rot fungus. In addition, pickers were frequently stung (yellowjackets feeding on the back side of the clusters were not seen), resulting in delays in harvesting.

Nearly identical problems are experienced with the grape crop and yellowjackets in Pennsylvania and New York. During 1976, many grapes in Pennsylvania were damaged, and many delays occurred in harvesting because pickers were stung. Unfortunately, no concrete data were collected on these incidents, but the problems were described as "considerable." The species involved were probably *V. maculifrons* and perhaps *V. germanica*. In New York, yellowjackets also cause some problems to grape growers (W. B. Robinson, Cornell Univ., personal commun.). The damage seems to be most extensive in small personal lots of grapes, and sweet, early ripening, tender-skinned varieties are the most susceptible. The yellowjackets sever the skin of the fruit to get at the juices. In some of these small plots, as much as 95 percent of early season grapes are lost to yellowjacket damage. Later varieties of grapes that ripen in cold weather are much less susceptible. Again, the species of yellowjackets involved has not been determined, but *V. maculifrons* and *V. germanica* workers are probably the principal pests, with some damage by workers of *Vespa crabro*.

In agricultural areas, it is probably the beekeeper who consistently experiences the most problems with yellowjackets. These problems are shared by beekeepers throughout the world. In New Zealand, they have combated depredations of *V. germanica* on their bee colonies since this yellowjacket was introduced into the country in 1945. During years of high yellowjacket populations, the wasps cause havoc and considerable financial losses to the industry. A survey by Walton and Reid (*1976*) revealed that 88.6 percent of the beekeepers they surveyed considered *V. germanica* a nuisance and 73.6 percent a cause of financial loss. During the 1975-76 season, *V. germanica* workers were estimated to have destroyed 3,900 colonies and partly affected more than 10,000 others.

In North America, beekeepers also experience financial losses due to colony destruction by yellowjackets, especially *V. pensylvanica* and *V. germanica*. The yellowjackets may also delay operations during honey extraction because of the apprehension or actual stinging of personnel at the apiary. Another, indirect, problem for beekeepers in many fruit-producing regions occurs when the yellowjackets pierce ripe pears, peaches, and other fruits. If there is a lack of nectar, large numbers of honey bees (which only occasionally pierce sound fruit) are attracted by the juices of the pierced fruit. This sometimes causes severe problems for fruit growers and pickers, and the apiarist may be asked to remove or control the hives.

Yellowjackets are also a problem for commercial Christmas tree growers, especially during pruning operations in midsummer. Laborers often do not see the nests on the opposite side of the tree until it is too late, and they are frequently stung repeatedly when the tree is vibrated.

Yellowjackets may become equally troublesome in logging and sawmill operations. During years of high yellowjacket populations in forests, operators of heavy equipment, such as graders, tractors, skidders, trucks, and loaders, are prone to attack from yellowjackets whose nests are disturbed by vibrations or displacement, and much time is lost while the wasps are controlled. Occasionally, workers at sawmills are troubled by yellowjackets. During the summer of 1973, during a "population outbreak" of yellowjackets in the Pacific Northwest, one sawmill near Wenatchee, Wash., closed after personnel at the mill refused to tolerate these insects any longer. The mill opened only after the workers were convinced that a control program was well underway. Similarly, a building contractor constructing a house near Moscow, Idaho, stopped all building until the future homeowner instituted control procedures for the extremely abundant yellowjackets. The delay was costly to both the contractor and the homeowner in lost wages, penalties, and time.

"In a recent 5-year period, insect stings accounted for over 5 percent of all Forest Service medical treatment and lost-time accidents" (Putnam, *1977*). These stings are especially numerous and frequent when Forest Service personnel are fighting forest fires. The firefighters are commonly stung and must be removed from the firelines as they encounter hordes of yellowjackets flying above their smoke-filled subterranean nests. The firefighters are also disturbed by yellowjackets during meals when the scavenger species are attracted to the food and juices being served. To partially alleviate these types of problems, the Forest Service has published a bulletin concerning the control of stinging and biting insects at campsites (Putnam, *1977*).

Losses in Recreational Areas

Everyone who has camped or picnicked at recreational facilities, especially in forested areas, is aware of the nuisance of scavenging yellowjackets. These pests are sometimes responsible for considerable financial losses to government agencies and private organizations that provide the facilities since attendance revenues are often drastically reduced during years of yellowjacket outbreaks. For example, during the 1973 outbreak in the Pacific Northwest, private, county, State, and Federal parks and recreation areas were nearly deserted. Revenue dropped considerably, and many bitter complaints about yellowjackets were received by the Forest Service, National Park Service, Bureau of the Interior, and the Army Corps of Engineers, all maintaining recreational facilities of one type or another in this area. In addition, resorts in northern Washington and Idaho lost considerable revenue until vigorous yellowjacket control programs were instituted. Poinar and Ennik (*1972*) estimated losses at certain resorts in California reached $5,000 annually per resort. Wagner and Reierson (*1969*) reported similar reductions in attendance at many recreational areas in southern California because of yellowjackets. Howell et al. (*1974*) stated that yellowjackets are considered one of the most serious pests in outdoor recreational areas in Georgia. Although yellowjackets undoubtedly create similar problems in other areas of North America, no additional information is available.

Officials of private organizations and governmental agencies providing recreational facilities are becoming increasingly concerned about finding better ways to protect their patrons from yellowjackets. They are especially concerned about persons hypersensitive to the venoms. Most are planning to increase their budgets to contain contingency plans for yellowjacket control programs.

Losses in Urban and Suburban Areas

During years of high yellowjacket populations, these wasps are responsible for economic losses in urban and suburban areas, just as they are in agricultural and recreational areas. These losses occur at city parks, playgrounds, zoos, amusement parks, and athletic facilities. The presence of large numbers of yellowjackets at these places causes considerable alarm among patrons and results in severely reduced attendance. Revenues from admissions drop proportionally. Operators of concession stands also suffer financially. Customers refuse to buy food and beverages since this material is highly attractive to yellowjackets. During 1973, the Portland, Oreg., zoo was experiencing all the above difficulties, but once an effort was made to cover all garbage cans in the area, to remove all food remnants, and to introduce a limited control program by baiting, the yellowjacket density quickly dropped to acceptable levels.

In some communities, yellowjacket problems are severe enough nearly every year to necessitate organized control programs. Often local, county, or State agencies provide important biological and ecological studies and attempt to control these pests. For example, one large county mosquito abatement district in California spent nearly 6 percent of its operational budget from 1969 to 1972 for evaluation and control of pestiferous yellowjacket species in their district.

Yellowjackets can also be a serious and costly occupational hazard to certain types of employees in cities and suburbs. Garbage collectors and operators of heavy equipment at municipal landfills and refuse dumps are sometimes repeatedly stung, requiring significant numbers of them to leave their jobs to seek medical attention. In 1973, during the peak populations of *V. pensylvanica* and *V. vulgaris* in the Pacific Northwest, personnel of one industrial accident insurance group became alarmed at the number of compensation requests they processed from employees stung by yellowjackets.

Other employees in urban-suburban areas affected by yellowjackets include workers at food canneries (several companies have reported costly delays); meat processing plants; jam, jelly, and pickle factories; and wineries. The most important single factor in many of these cases is not the stinging, but the annoyance factor and the threat of being stung. The employees are frightened of yellowjackets, and it affects their work greatly.

Personnel at military bases, often located in or adjacent to suburban areas, also encounter problems with yellowjackets, especially at mess facilities and garbage collection sites.

The greatest number of yellowjacket problems occur with homeowners on their own property. With the increased interest in barbecues and outdoor cooking, the number of encounters with yellowjackets has increased. Many people claim they are unable to enjoy their own yards during outbreak years, and are greatly annoyed during typical years. Although some effective control procedures are available to homeowners, many employ pest control specialists to achieve control, especially when the yellowjackets build their nests in or close to their homes.

Although, during certain years, yellowjackets are responsible for large economic losses in agriculture, in recreation industry, and in the urban-suburban environment, it should be stressed that most people are terrified of Hymenoptera and yellowjackets in particular. There is no way to determine the economic value of this stress upon people, but its importance must be recognized.

MEDICAL IMPORTANCE

Yellowjacket Sting Apparatus

Morphology

Although cartoonists delight in portraying the sting or "stinger" of wasps and bees as a constantly protruding spike, the real sting is part of a complex apparatus hidden in a cavity at the end of the abdomen. It is actually a modified ovipositor, or egg-laying device, which comprises the external genitalia of many female insects. The visible portion of a typical ovipositor consists of three pairs of more or less elongate structures, or valves, which are used to insert the eggs into a substrate such as plant tissue or soil. One pair of valves often serves as a sheath and is not a piercing structure; the other two pairs form a hollow shaft, which pierces the substrate by a back and forth sawing motion of one pair held in position by the other. The eggs then pass down through the shaft. Accessory glands (usually two) within the body of the female often inject secretions, through the ovipositor, which form egg pods or glue the eggs to the substrate.

In aculeate Hymenoptera, the ovipositor has become a stinging device that no longer functions in egg laying. The genital opening (gonopore) from which the eggs pass is anterior to the sting apparatus, which is flexed up out of the way during oviposition. The accessory glands have also been modified: One has become a poison gland ("acid" gland); the function of the other (Dufour's or "alkaline" gland) is unknown, although it may be associated with the production of pheromones.

Detailed discussions of the origin of insect genitalia (including ovipositors) and their relationships to other appendages were presented by Smith (*1969*, *1970*). The morphology and function of the venom apparatus of Hymenoptera was discussed by Maschwitz and Kloft (*1971*), and a specific discussion of the yellowjacket sting apparatus was presented by Spradbery (*1973a*).

As shown in figure 66, the sting apparatus in its normal, retracted position is located between abdominal tergum 8 (a small sclerite concealed beneath tergum 7) and sternum 7. In figures 67 and 68, the apparatus is illustrated with the hoodlike tergum 8 removed. Each side consists primarily of three plates. Figure 67 illustrates these paired plates ventrally, and figure 68 depicts one-half of the apparatus from the side. From each small *triangular plate* (gonocoxite 8 or valvifer I), arises a long, slender *lancet* (gonapophysis 8 or valvula I). The triangular plate articulates ventrally with a large *oblong plate*

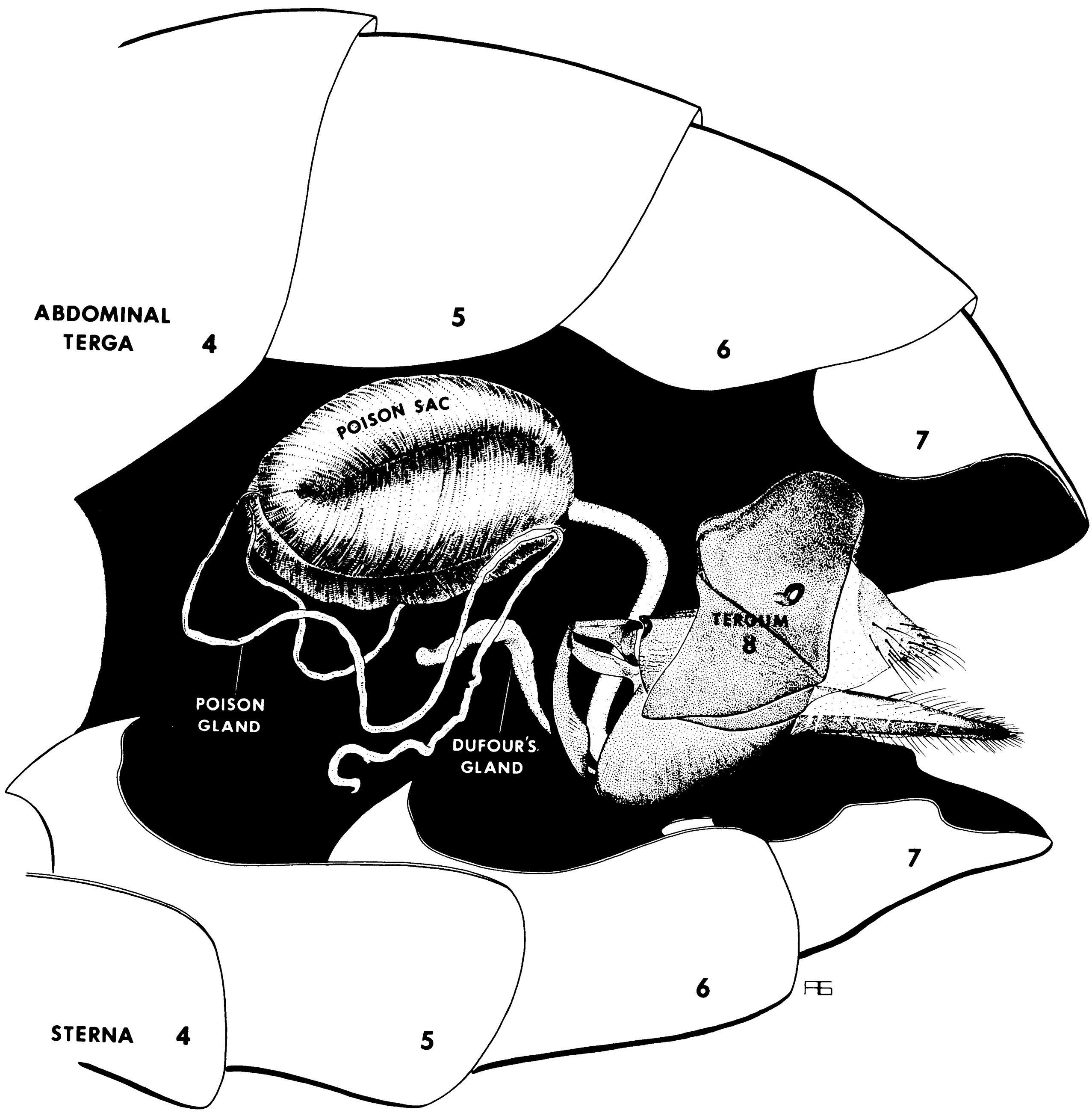


FIGURE 66 — Yellowjacket worker abdominal terga and sterna pulled apart to show location of sting apparatus (relaxed position—only one-half visible) and associated glands. The sting, that is, shaft of stylet plus lancets, is partly visible behind the semitransparent sting sheath.

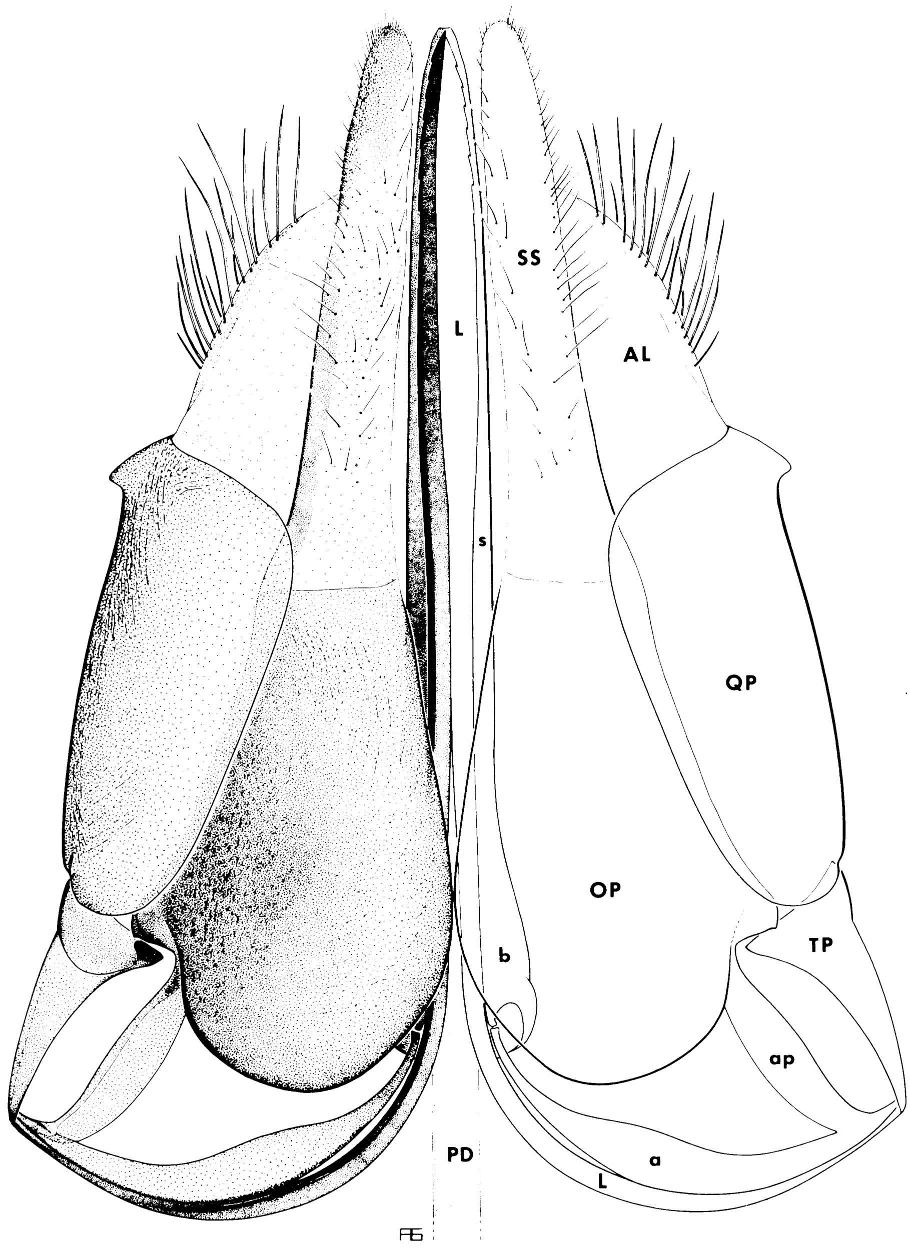


FIGURE 67 — Ventral view of relaxed yellowjacket worker sting apparatus, partially flattened out. Compare with lateral view of one-half of apparatus, figs. 66 and 68*a*). Note that the lancet on the right (unshaded) overlaps the one on the left (shaded) shortly after they converge.

Abbreviations for figures 67 and 68

OP	oblong plate	SS	sting sheath
QP	quadrate plate	L	lancet
TP	triangular plate	s	shaft of stylet
ap	anterior process of oblong plate	b	bulb of stylet
PD	poison duct	a	basal arm of stylet
AL	anal lobe		

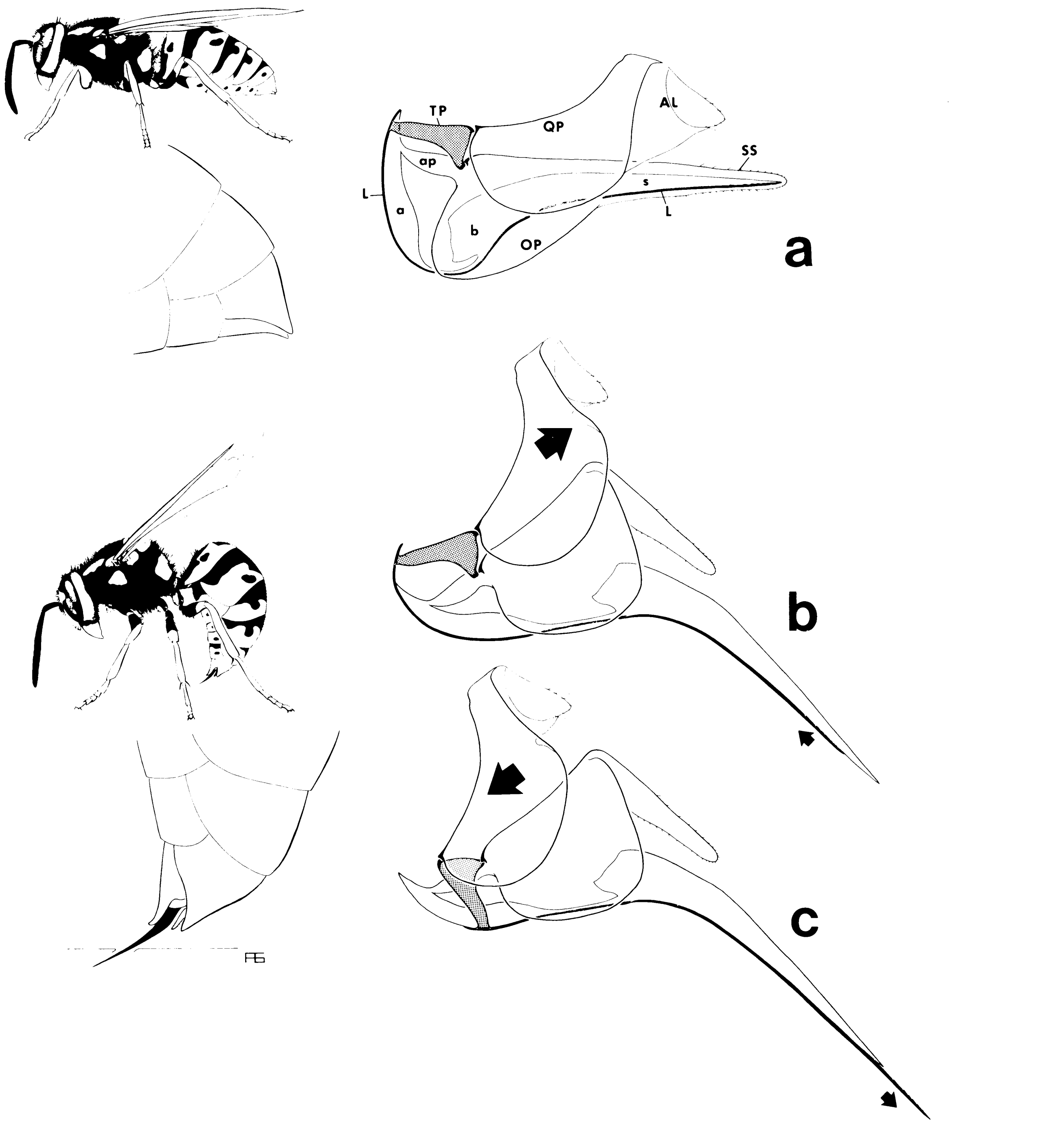


FIGURE 68 — Semidiagrammatic lateral views of one-half of yellowjacket worker sting apparatus, eighth tergum removed. Nonagitated and stinging yellowjackets with enlarged apical gastral segments also illustrated. *a*, Sting fully retracted and concealed behind oblong plate and sting sheath in normal, relaxed position within body of wasp. *b*, *c*, Sting at maximum thrust. Both quadrate and oblong plates are displaced upward. As the sting slides against the inner surface of the curved oblong plate, it pulls on the plate's lower edge, flattening the plate somewhat and thus broadening its lateral configuration. At the apex of the oblong plate, the flexible sting sheath is bent downward and parallels the sting. *b*, Quadrate plate shifted posteriorly, triangular plate (shaded) rocked upward, lancet retracted. *c*, Quadrate plate shifted anteriorly, triangular plate rocked downward, lancet extruded. (See fig. 67 legend for explanation of abbreviations.)

(gonocoxite 9 or valvifer II). From an anterior process on the oblong plate arises a basal arm of the *stylet* (gonapophyses 9 or valvulae II): these arms fuse into a swollen, hollow *bulb*, which then narrows into a tapering *shaft*. The stylet interlocks along its entire length with the two lancets, which slide freely along its ventral edges. Where they converge at the bulb, they form a channel with the shaft through which the poison flows. As seen in figure 68, the oblong plates overlap the sting bulb and part of the shaft. The distal ends of the plates are prolonged into *sting sheaths* (gonostyli 9 or valvulae III), which laterally cover the remainder of the sting shaft when it is retracted.

The remainder of each half of the apparatus consists of a large *quadrate plate*, modified from abdominal tergum 9, which overlaps the oblong plate and, like the latter, articulates with the triangular plate. A hair-covered *anal lobe* derived from the tenth abdominal segment is connected by a membrane to the posterior of the apparatus. The poison gland consists of two slender filaments which arise from one end of a prominent, heavily muscled reservoir, or poison sac (fig. 66). This in turn empties, via a narrow neck, into the sting bulb, as does Dufour's gland (fig. 67).

Sting Function

An attacking yellowjacket grips firmly with its legs (the hornet, *Vespa crabro*, often holds on with its mandibles as well), elevates the oblong and quadrate plates to expose the sting, then plunges the tip of the interlocked lancets and stylet into the skin with a downward thrust of the abdomen. Simultaneously, contraction of the poison sac muscles injects the venom into the sting bulb and through the channel formed by lancets and shaft, much like a hypodermic needle; however, penetration is not a matter of a single stroke. The curious person who inspects a bee or wasp for the first time is usually surprised at how flexible the sting is and the difficulty in piercing human skin with it once the insect is dead. As shown in figure 68, on each side of the apparatus the quadrate plate rapidly moves back and forth during stinging, pivoting the triangular plate on its articulation with the oblong plate. The lancets attached to the triangular plates are thus displaced forward in alternate strokes, each sliding on its track against the shaft. The tips of the lancets are equipped with tiny barbs to facilitate penetration, and as shown in figure 69, they literally saw through the victim's flesh as each in turn is thrust forward and anchored in place by the barbs. Thus, the action of the sting closely resembles that of many ovipositors during egg laying. (The barbs on a yellowjacket or hornet sting are much smaller than those of the honey bee. Consequently, the sting does not normally become fixed in a person's flesh, and the wasp may quickly withdraw with a upward pull of its abdomen and sting again.)

Venoms

Most aculeate wasps are solitary and use their stings primarily for subduing prey. Their venoms are also specialized for this purpose and most cause slight and temporary pain to humans. The social Vespidae (including yellowjackets), however, use the sting primarily as a defensive weapon, and the venom contains materials that cause intense pain to vertebrates.

Yellowjacket venoms were investigated by Geller et al. (*1976*), Habermann (*1972*), and Yoshida et al. (*1976*). Feingold (*1973*) discussed the materials present in the venom and their action on the human body. Table 12 lists the active constituents of wasp (yellowjacket), bee, and hornet (*Vespa crabro*) venoms. A more complete listing, by species, was compiled by Geller et al. (*1976*).

Yellowjacket venoms are highly complicated mixtures of pharmacologically or biologically active agents or both (Habermann, *1972*). These agents cause the contraction of smooth muscle, stimulate glands of external secretion, increase capillary permeability, produce vasodilation with a resulting fall in blood pressure, destroy normal tissue barriers, and cause intense pain. The effects of individual constituents were given by Feingold (*1973*).

Yellowjacket Stings

Prior to the 1960's, literature on Hymenoptera as medically important insects was meager, and their capabilities to cause death of humans was

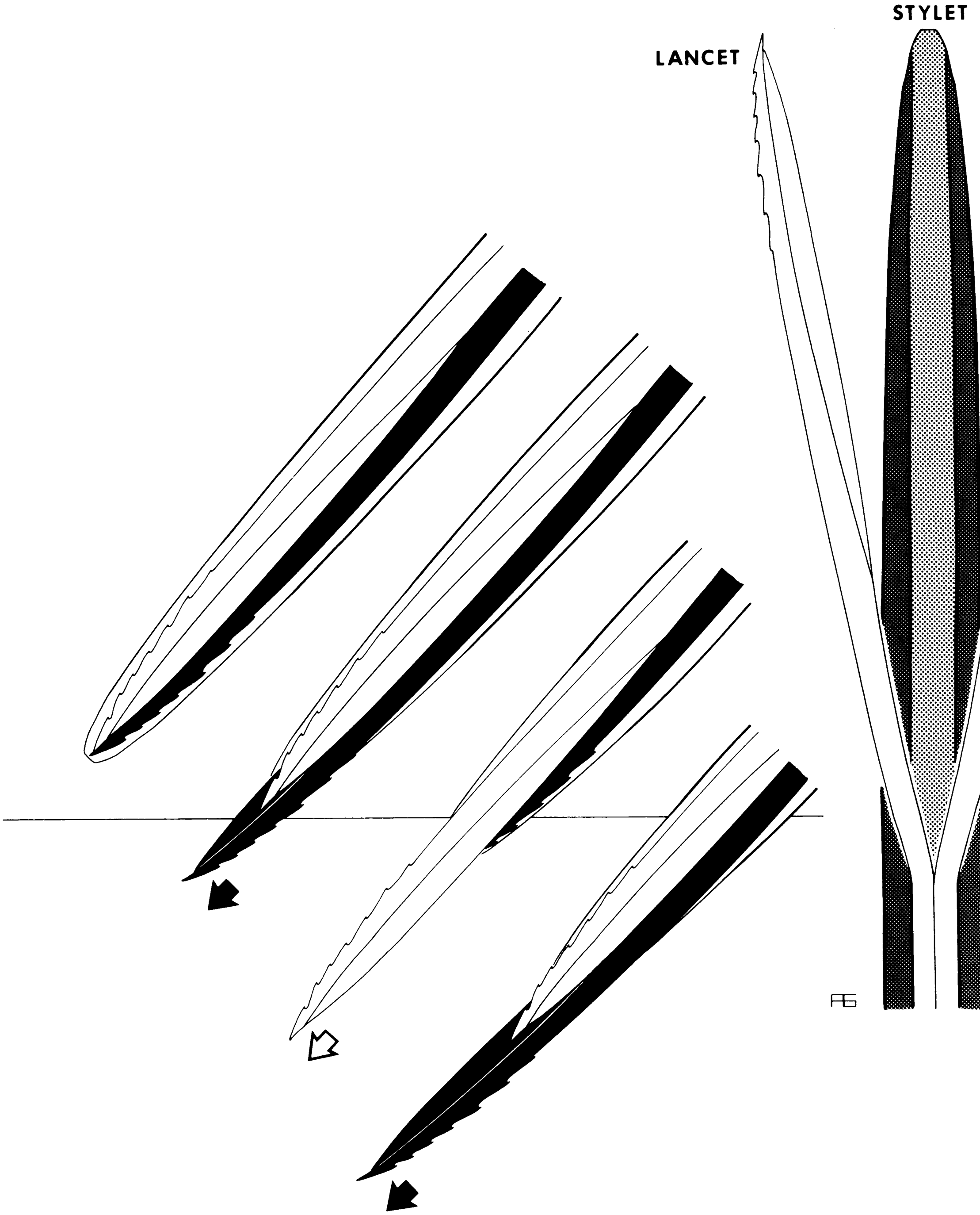


FIGURE 69 — Ventral views of sting tip showing: sting penetration by alternate forward strokes of the lancets, sliding along the shaft of the stylet, and lancets pulled out of their track on the shaft. Although the lancets lie side-by-side for a short distance after converging at the base of the shaft, their expanded, bladelike ends overlap at the tip. The facing blade surfaces are each concave, creating a tubular poison channel between them.

TABLE 12.—*Pharmacologically and biochemically active constituents of wasp, bee, and hornet venoms (modified from Habermann,* 1972) [+, present; −, absent; ?, questionable]

Substance	Wasp	Bee	Hornet
	Biogenic amines		
Histamine	+	+	+
Serotonin	+	−	+
Dopamine	+	+	−
Noradrenalin	+	+	−
Acetylcholine	−	−	+
	Protein polypeptide toxins (nonenzymatic)		
Melitten	−	+	−
Apamin	−	+	−
MCD peptide	−	+	−
Minimie	−	+	−
Kinins	(1)	−	(2)
	Enzymes		
Phospholipase A	+	+	+
Phospholipase B	+	?	+
Hyaluronidase	+	+	---

[1]Vespula kinin.
[2]Hornet kinin.

largely undocumented. More recent reports, such as those by Parrish (*1959, 1963*), Leclercq and Lecomte (*1975*), and Lecomte and Leclercq (*1973*), have drawn attention to the medical importance of Hymenoptera. Parrish (*1963*) analyzed fatalities due to venomous animals in the United States from 1950 to 1959. The study revealed that 229 of 460 recorded deaths were due to the stings of hymenopterans such as yellowjackets, other wasps, ants, and bees. Barnard (*1973*), in a publication of reports of the Insect Sting Subcommittee of the American Academy of Allergy, reported more than 400 fatal reactions in a 10-year period due to one or more stings. The reports indicated four main types of pathology were responsible for the fatalities. One hundred autopsies revealed 69 deaths were due to respiratory problems, 12 due to anaphylactic shock, 12 to vascular involvements, and 7 to neurological problems. One to 2 percent of the 400 fatalities were attributed to bacterial septicemia. Benton and Heckman (*1969*) suggested that most infections probably result from scratching the wound site, although there is a possibility stinging insects may transmit pathogenic micro-organisms by way of the sting.

Although Parrish (*1963*) used death certificates for some of his information, Fluno (*1961*) suggested such documents do not include all deaths due to wasp stings. He pointed out that reactions to stings are not even categorized in morbidity reports at some hospitals; a code is used which combines all types of venoms including those of snakes, scorpions, wasps, and spiders. Parrish (*1959*) was of the opinion that many coroners are not aware of anaphylactic shock as a cause of death; therefore, many deaths reported as heart attacks or heat strokes may have been caused by hymenopteran stings. For these reasons, the exact number of fatalities caused by yellowjackets is unknown; however, it is probably much higher than suspected.

In recent years, there appears to be an increasing amount of interest and concern about yellowjackets by the general public. Much of this concern probably stems from increased encounters with these wasps due to the present emphasis on outdoor activities such as camping, picnicking, and hiking. Fluno (*1961*) stated that about half of the 10,000 requests for information about wasps and their control received yearly by USDA were accompanied by statements that one or more members of the family reacted severely to wasp stings. Although there are no recent data on the number of requests received yearly, the number has apparently increased greatly. In addition, thousands of requests for information on wasps are received by universities and other State and Federal agencies.

There has also been a corresponding awareness on the part of physicians and other medical researchers of problems related to hymenopteran stings. This has resulted in a number of papers on various aspects of these subjects, which were reviewed and listed for 1953-70 by Barr (*1971*) and for January 1970 to November 1972 by Nowak (*1972*).

Fatal Reactions to Stings

Great variability exists among individuals in their reactions to insect stings; however, a considerable amount of information has been published on the subject, which provides a better understanding of the medical problems involved.

Zeleznick et al. (*1977*) were of the opinion that relatively few deaths occur from anaphylactic shock due to stings by wasps, hornets, yellowjackets, and bees; however, they noted estimates of 0.4 to 0.8 percent of the population that experienced a systemic reaction to stings. Therefore, the potential for these types of reactions is great (Frazier, *1976*). Perlman (*1962*) found severe reactions to arthropod bites and stings statistically no more frequent in patients with general allergic disorders than in the general population, nor were they correlated with heredity.

Symptoms of Allergic Reaction

Feingold (*1973*) reported the following symptoms concerning local reactions to a sting (fig. 70). He stated, "Immediately following the sting, intense burning is experienced at the site of the sting to be followed after several minutes by swelling and intense itching. The swelling may be localized to a few centimeters immediately surrounding the sting or the edema may involve an entire extremity or other segment of the body."

Symptoms of a generalized systemic reaction may range from mild to severe. Frazier (*1976*) stated, "Such reactions can be delayed, presenting serum sicknesslike symptoms of fever, headache, malaise, urticaria, lymphadenopathy, and polyarthritis. It is an immediate reaction, however, that presents the physician with a medical emergency. Even a slight systemic reaction with symptoms of generalized urticaria, itching, malaise, and anxiety should be assessed and treated on a long-term basis in the realization that the next time the patient is stung the results may be far more serious, even life-threatening.

"A moderate systemic reaction may be marked by any of the symptoms mentioned and two or more of the following: (1) constriction of throat or chest, (2) abdominal pain, nausea, vomiting, (3) dizziness, (4) wheezing, and (5) generalized edema.

"A severe systemic reaction may include any of these symptoms and two or more of the following: (1) labored breathing, (2) difficulty in swallowing, hoarseness, or thickened speech, (3) weakness, (4) confusion, and (5) a feeling of impending disaster.

"A shock or anaphylactic reaction would exhibit any of these symptoms in addition to two or more of the following: (1) lowered blood pressure, (2) cyanosis, (3) collapse, and (4) incontinence and unconsciousness."

While immediate reactions are an instant cause for concern, delayed reactions resulting in death may occur several hours after the sting. Bukantz (*1975*) cited the results of 100 autopsies that showed 59 of the deaths occurred within 60 min, 22 between 1 and 6 h, 7 between 6 and 96 h, and 9 after more than 96 h. The interval of time before death was unknown for three of the victims.

PN–6547

FIGURE 70 — Localized sting reactions to *Vespula pensylvanica: a,* Swollen foot about 6 hours after 2 stings by a single worker; *b,* sting blister on ankle, 4.2 × 2 × 1.5 cm high, 36 hours after being stung twice by a single worker. This is a primary reaction, not a secondary infection.

Ancillary Factors and Sting Fatalities

Ancillary factors, such as age of victim, type of insect involved, and the number of stings, were presented by Barnard (*1973*). From 100 postmortem cases, it was determined that 64 were under 50 years of age. "Bees" were responsible for 44 of the deaths, "wasps and hornets" for 26, "yellowjackets" for 18, and stings of unknown origin for 12. Since identifications of the stinging insects are usually unreliable, these figures should only be taken as rough estimates. These data showed 78 of the victims had 1 to 4 stings, 16 had more than 4; 43 percent of the stings were on the head and trunk, 27 percent on the extremities, and 9 percent on the trunk.

Emergency Treatment

Frazier (*1976*) stressed that the most important step in treating systemic reactions is the immediate subcutaneous injection of 0.2 to 0.5 ml of epinephrine (1:1000) for an adult and not more than 0.3 ml for a child. Feingold (*1973*) advised epinephrine injections for all patients with a history of previous stings since a previous mild reaction is no index of severity of subsequent reactions. He stated, "For epinephrine to be effective, it must be administered immediately without waiting for the development of symptoms. Once the reaction is established, reversal is very difficult. If signs and symptoms develop following the initial dose, repeat the epinephrine within fifteen to twenty minutes." Barnard (*1973*) reported that 67 percent of the patients whose sting was severe but nonfatal had received early treatment with aqueous epinephrine. He also mentioned an appreciable number of fatal reactions where isoproterenol had been the sole treatment.

Cold compresses at the site of the sting prevent rapid dissemination of toxin and relieve, at least to some extent, the immediate burning sensation and pain. Other immediate treatments include applying a proteolytic enzyme (such as household meat tenderizer) to the sting site. This offers some relief as do commercial preparations. Antihistamines may be administered orally or parenterally; however, they should not be used as a substitute for epinephrine (Feingold, *1973*).

Long-Term Treatment

Anyone experiencing any of the symptoms of sensitization to stings should seriously consider desensitization procedures. Frazier (*1976*) stated "the physician's responsibility . . . does not end with the successful treatment of the acute episode. The patient is totally vulnerable and may die quickly if stung again. Desensitization should be begun at once."

Desensitization involves injection of extracts made from entire insects (Frazier, *1976*) or injections prepared from pure venom (Lichtenstein, *1975*; Sobotka et al., *1976*; Zeleznick et al., *1977*). However, there was some controversy over which method was better (Reisman, *1975*). Frazier (*1976*), who uses the whole-body extract, recommended that a severely allergic patient be kept on maintenance dosage indefinitely rather than for a set period since there is no good knowledge on the permanence of this desensitization procedure. Hunt et al. (*1978*) have shown that pure venom is superior to whole-body extracts for desensitization.

Emergency Medical Kits

Most allergists recommend epinephrine syringe kits for immediate treatment when professional medical help is not available. For example, Frazier (*1976*) prescribes an insect sting kit for his patients, who are instructed to keep it with them at all times. The kit contains a preloaded syringe of epinephrine, antihistamine tablets, and several tablets of phenobarbital. Similar kits are now available commercially if prescribed by a physician. In addition to a syringe of epinephrine, these kits contain antihistamine tablets and/or an inhaler that contains an effective bronchodilator. Directions for use are present in each kit.

This type of kit should be a standard item in first aid supplies at public facilities such as campgrounds and parks. Persons entrusted with the public safety, such as scout leaders, forest rangers, park service personnel, lifeguards, and golf and tennis professionals, should be instructed how to recognize severe allergic reactions and how to administer the medications provided in the kit (Frazier, *1976*). Persons with severe allergic reactions to stings should also wear a medical warning bracelet and carry a similar card in their wallet.

Avoidance of Stings

Reisman (*1975*) suggested several simple measures that help avoid stings. They include: (1) Not wearing perfumes, hair sprays, suntan lotion, and cosmetics, as yellowjackets are often attracted to these compounds; (2) wearing light-colored clothing such as white and tans; (3) not walking barefoot outside; (4) exercising care when gardening, mowing a lawn, and cutting shrubbery; and (5) avoiding outdoor cooking and eating during the yellowjacket and bee season.

Even more important than the above, people should try to remain calm in the presence of yellowjackets. If wasps are gently brushed off the body when they alight instead of being swatted, chances of being stung are reduced considerably. When yellowjackets are present at picnic tables, the same principle holds: Move slowly and deliberately instead of rapidly, and the wasps will rarely sting. When a yellowjacket is discovered in a moving automobile, the car should be driven off the main road quickly and the wasp removed or killed. It usually poses no threat to the driver as long as all movements are careful and unhurried.

CONTROL

Even though most yellowjackets are beneficial, when aerial nesters build their nests in inconvenient locations, or when populations of scavenger species reach intolerable levels, control measures must be employed. It is often difficult to determine when population levels are high enough to warrant control since some people tolerate large numbers of yellowjackets whereas others are alarmed at the sight of a single worker.

MacDonald et al. (*1976*) noted that when abatement becomes necessary, there are two general approaches of control—destruction of individual yellowjacket colonies and area-wide abatement of worker populations. Akre and Davis (*1978*) listed nest destruction, use of poison baits, proper management of garbage, and trapping with synthetic lures as being the most commonly used methods of abatement. Other useful methods employ the use of baits over water containing a wetting agent and traps using fish or other meat as bait.

Nest Destruction

Destruction of colonies within the nest remains one of the principal methods of controlling yellowjackets, especially by homeowners. The best time for control is after dark when foraging activity has ceased, and the maximum number of workers are in the nest.

Subterranean Nests

Research data indicate that subterranean colonies are easily killed by pouring insecticides such as propoxur (1.5 lb per gallon emulsifiable concentrate at the rate of 8 oz per gallon of water) or carbaryl (5 percent dust) into the entrance hole, which is then plugged with cotton or similar material. If the plug and immediate area are saturated with insecticide, foragers that have spent the night elsewhere will return in the morning and contact this material. Research results also show that aerosols containing pyrethrins, rotenone, and a cooling agent (to lower body temperature) are also effective in controlling subterranean colonies if the nest is fairly close to the entrance hole.

Nests in Houses

Yellowjackets nesting in between walls of houses or other structures make control difficult. Morse et al. (*1977*) described the tendency of *V. germanica* to nest within the walls of houses in New York and cautioned homeowners not to block the entrance hole as the yellowjackets may chew through the interior walls to escape. *Vespa crabro, Vespula maculifrons, V. squamosa, V. vidua* (J. Nixon, Silver Spring, Md., personal commun.), *V. pensylvanica*, and *V. vulgaris* also frequently build nests in houses; other species, to a much lesser extent. Because control of these colonies is difficult, the homeowner may wish to seek professional assistance.

One effective method of treatment, indicated by research results, involves the use of a synthetic pyrethroid and carbaryl dust (J. Nixon, Silver Spring, Md., personal commun.). The plastic wand of the aerosol generator containing the pyrethroid is quickly placed into the entrance hole, and 3.5 to 10.5 g of the material are released during a 10- to 30-sec burst. The entrance hole is then plugged with steel wool, and the wool and surrounding area are dusted with about one ounce (28 g) of 5 percent carbaryl. This method has the advantage that treatment can take place during the day; returning foragers chew at the steel wool coated with insecticide dust and succumb quickly. Protective clothing (bee suit, veil, gloves) should be worn during the entire operation. Although Morse et al. (*1977*) recommended the entrance hole not be plugged, this pertained only to healthy colonies, not to those being treated with insecticides. With the control method outlined above, there is little danger of workers chewing a new exit and emerging inside the house. Workers from only 1 of 50 nests treated in this manner were able to find or create a new exit, and, even then, less than 10 workers were found dead in a closet below the nest.

Aerial Nests

Colonies of yellowjackets in aerial nests may be killed by using one of several recently developed aerosol products that contain a quick knockdown insecticide (Davis, *1978*). The toxicants are propelled distances of 3 m (10 ft) or more by the aerosol. Nests of this type may also be sprayed with propoxur (1.5 lb per gallon emulsifiable concentrate at the rate of 8 oz per gallon of water).

Use of Poison Baits

When a mixture of insecticide and bait is used for control, yellowjacket workers collect the bait at stations placed in the field, carry it back to the nest, and the material is then distributed to other members of the colony by trophallaxis (MacDonald et al., *1976*). Death of the colony usually occurs within 2 weeks.

The use of a bait combined with an insecticide is an old technique, having been in use at least 40 years ago in Washington when lead arsenate was used as the toxicant. About 1950, a wettable powder formulation of chlordane became available and this material, together with a fish or beef bait, was very effective against *V. pensylvanica* (C. A. Johansen, Wash. State Univ., personal commun.). The first program of yellowjacket control, utilizing a nonrepellent, persistent insecticide in conjunction with meat baits, was proposed by Grant (*1963*). Later, Grant et al. (*1968*) published the results of a 5-year testing program that utilized cooked horse meat and chlordane. This material effectively controlled populations of *V. pensylvanica* and *V. vulgaris* in parks and suburban areas in San Mateo County, Calif. Wagner and Reierson (*1969, 1971b*) also reported excellent control of *V. pensylvanica* in parts of southern California using a mixture of fish-flavored cat food and mirex, a slow-acting insecticide, used in conjunction with a chemical attractant. Similar programs have been tried by Keh et al. (*1968*) and Rohe and Madon[12] in California.

To be acceptable, the insecticide must not be repellent to yellowjackets, and it must be relatively slow acting so that it can be distributed throughout the colony by trophallaxis.

The most promising new material, tested and evaluated by Ennik (*1973*), is an encapsulated formulation of diazinon mixed with tunafish cat food. Using this bait at eight test sites in northern California, foraging worker populations of *V. pensylvanica* and *V. vulgaris* were reduced an estimated 75 to 90 percent within 2 days of exposure to the bait. The effectiveness of this material is due in part to the microencapsulation of the diazinon in a plastic material that masks its repellent odors. According to F. Ennik (Calif. Heath Dept., personal commun.), the technique of microencapsulation of insecticides will make available many compounds that are extremely repellent to yellowjackets but are relatively safe to use and are biodegradable. He also noted that preliminary tests with microencapsulated insect growth regulators appears promising as an alternate to the use of insecticides.

Encapsulated diazinon is registered for use in a bait formulation in California and Washing-

[12]Rohe, D.L., and M.B. Madon. A field evaluation of mirex and chlordane poisoned baits for the control of the ground-nesting yellowjacket *Vespula pensylvanica* (Saussure), on Santa Catalina Island, Calif. Progress Report. 1968. Calif. Dept. Pub. Health, Bureau Vector Control. 11 p. 1969. [Mimeographed]

ton. Only the insecticide is available commercially, bait is provided by the user. One teaspoon of the insecticide is mixed with 6 oz of a suitable meat bait (cooked meats, tunafish, and various cat foods). The poisoned bait is then placed in a container constructed to permit foraging yellowjackets access, but to exclude birds and small animals (fig. 71). The container(s) is then placed (perhaps suspended from a tree branch or placed on a platform) in the area in which control is desired. Every 2 or 3 days the bait must be replaced as yellowjackets will not scavenge spoiled meat. More explicit directions are included with the insecticide.

MacDonald et al. (*1976*) listed several advantages of using poison baits for yellowjacket control, which included the following: (1)Specificity for the target species (pestiferous scavengers) without disturbance to the beneficial, strictly predaceous species; (2) minimal contamination of the environment; (3) elimination of the need to locate individual yellowjacket colonies for destruction; (4) possible control of the yellowjackets early in the season before populations reach a nuisance level; and (5) destruction of colonies before the development of new reproductives late in the season.

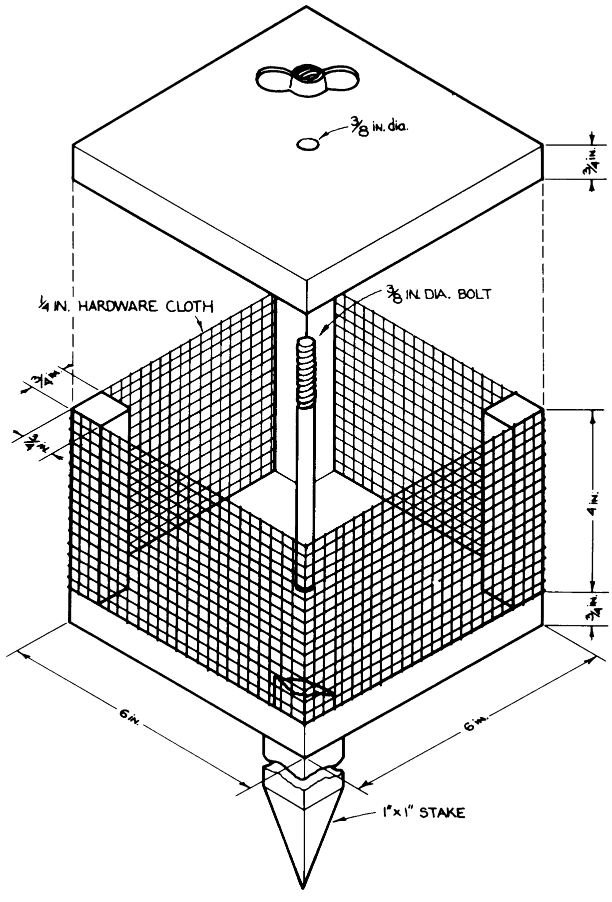


FIGURE 71 — Dispensing station for insecticide-treated meat bait (S. Peck). The 1- × 1-inch stake can be made any height, but 36 to 40 inches places the station at a convenient height. The top is removable to replace the meat. Yellowjackets can pass through the hardware cloth with ease, whereas children, pets, and wild animals are prevented from coming into contact with the bait.

Although several poison bait programs have apparently been succesful, nearly all have been restricted to the abatement of a single species, *V. pensylvanica*, and only in California. The pestiferous species in the Eastern States, such as *V. maculifrons* and *V. squamosa*, are unaffected by this technique as they are apparently not attracted to the baits currently in use. Effectiveness of this method of control on *V. vulgaris* outside California is unknown, but the workers of this species are attracted to protein baits. Similarly, little is known about abatement possibilities for *V. germanica* using the poison bait technique since this species has only recently become a serious problem and no testing has been done. Perrott (*1975*) found a mixture of mirex and canned fish substantially reduced worker populations of this species in certain areas of New Zealand; however, other researchers report that the overall abatement program in New Zealand is not as successful.

MacDonald et al. (*1976*) suggested the failure of this technique can be attributed mainly to pest species being differentially attracted to the baits. This necessitates the development of attractive, long-lasting baits specifically compounded for each pest species. Even after attractive baits have been found and a control program is initially successful, commercial processing may alter the original attractiveness (Rogers, *1972*). Another factor greatly influencing the success of these programs is the different biotypes of species occurring in different areas. For example, colonies of *V. pensylvanica* in southern California appear heavily committed to scavenging, whereas colonies of this species in Washington and Idaho, while still pestiferous, are not so totally committed to this method of obtaining protein. This greatly influences the acceptability of baits and, therefore, abatement by the poison bait method.

Chemical Lures

Davis et al. (*1967*) discovered that the synthetic material 2,4-hexadienyl butyrate was a highly specific attractant for the western yellowjacket, *V. pensylvanica.* Another material, heptyl butyrate, was discovered to be even more attractive and was used in small (87 oz) carton traps positioned on the periphery of a 22-acre peach orchard in Oregon to effectively depress yellowjacket worker populations so that fruitpickers could resume harvesting (Davis et al., *1973*). Abatement of the population to this level occurred within 4 days. In similar experiments at highway rest stops and overnight campsites along the Columbia River in Oregon and Washington, use of attractant traps baited with this synthetic lure depressed *V. pensylvanica* worker populations below troublesome levels.

Difficulties with the attractant trapping technique are similar to those experienced with poisoned baits. Attractants presently available are effective only for the western yellowjacket, *V. pensylvanica.* Other pest species, especially those in the Eastern States, are only slightly attracted (Grothaus et al., *1973*; Howell et al., *1974*). In addition, perimeter trapping with attractant traps has been effective only in areas limited in size (20 to 30 acres) and only in specific localities such as the orchards described by Davis et al. (*1973*). Heptyl butyrate seems to be most attractive to yellowjackets when used in dry areas with low humidity. These synthetic lures are highly attractive to workers and queens of beneficial, strictly predacious species, such as *V. atropilosa*, and trapping should be timed to minimize the number of individuals of these species that are caught (MacDonald et al., *1973*).

Although a commercial trap is available, attractant trapping with synthetic lures is not an effective control or abatement technique for the homeowner. One or two traps placed in a yard will not lower the worker population enough to alleviate problems, but may create an added hazard for residents by exposing them to additional yellowjackets attracted into the area. If this technique is ever to become an important consideration in abatement programs, additional, highly specific lures will have to be developed or discovered for all major pest species. In addition, these attractants will have to be effective over a wider range of environmental conditions so that they will be useful in most areas of North America.

Additional uses of synthetic yellowjacket attractants include the use of this technique as a monitor for colony growth, to estimate the number of workers in an area, or to increase the number of workers visiting poison baits. Figure 72 shows a good correlation between numbers of workers caught in attractant traps and colony growth in the field. Similar data, collected from specific localities, could be used in intelligent control programs to create the least disturbance to beneficial species and to time selected control procedures for maximum effectiveness against pest species. Ennik (*1973*) used traps baited with heptyl butyrate to monitor *V. pensylvanica* populations that had been subjected to poison bait formulations, and Wagner and Reierson (*1969*) found the addition of heptyl crotonate to poisoned bait tripled the amount removed by yellowjacket workers.

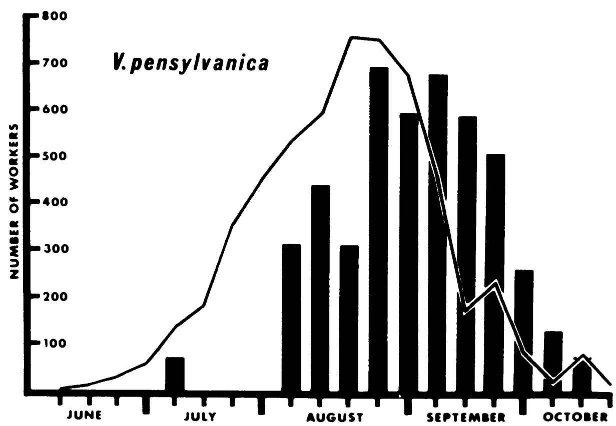


FIGURE 72—Weekly heptyl butyrate trap collection and weekly averages from excavated colonies. Each station on the abscissa represents 1 week (MacDonald et al., *1974).*

Management of Garbage

The proper management of garbage denies scavenging yellowjacket workers a readily available source of protein that could have been used to feed larvae during the period of exponential growth of the colony. When workers are forced to forage mostly for live prey, the colony probably does not grow as rapidly since more time is spent to feed each larva.

Morse et al. (*1977*) determined over 80 percent of the yellowjackets collected on food and garbage in and near restaurants and parks in Ithaca, N.Y., were *V. germanica*, a species notorious for its scavenging habits. Similarly, most of the hordes of *V. pensylvanica* workers pestering patrons of the Portland, Oreg., zoo in 1973 were attracted into the area by garbage in numerous cans with no, or ill-fitting, lids. A general policing of the area and a limited control program alleviated much of the problem. In southern California, Wagner (*1961*) found that treating trash containers once a week with an aqueous spray of 0.75 percent dichlorvos at picnic sites reduced *V. pensylvanica* worker populations to about 1 percent of those in untreated test areas. Akre and Retan (*1973*) also reported the effectiveness of dichlorvos strips attached to the inside of garbage can lids.

Biological Control

Biological control of yellowjackets shows little promise as an abatement method (MacDonald et al., *1976*). Spradbery (*1973a*) described parasites, predators, and pathogens as having little effect on yellowjacket populations. Biotic agents only have an effect in weakened colonies, levels of parasitism are low, and only small numbers of colonies are affected. He suggested that regulation of yellowjacket populations on an annual basis would require that colonies be weakened or destroyed before queen production was initiated.

A neoaplectanid nematode was investigated by Poinar and Ennik (*1972*) as a possible biological control agent, but the propagation of this parasite requires 100 percent relative humidity. Since this condition is not met in yellowjacket colonies, this agent is of limited use. Therefore, no biological control agent for yellowjackets exists, and this method of control is considered totally infeasible at the present time.

Control of Yellowjacket Queens

Spradbery (*1973a*) cited two attempts to regulate yellowjacket populations by the destruction of hibernating queens. In New Zealand, a bounty was paid for each *V. germanica* queen sent to the Department of Agriculture (Thomas, *1960*). A similar project was carried out in Cyprus. Results of both projects showed that mass destruction of queens had virtually no effect on yellowjacket populations the following summer. Spradbery thus remarked, "It is evident from the study of wasp populations that, with a mortality of 99.9 percent of potential queens and incipient colonies being necessary to maintain the same annual number of colonies, the destruction of winter queens is likely to have little or no effect on wasp populations. Indeed, a culling of winter queens may even cause an increase in the number of wasp nests by reducing the competition for suitable nest sites in the spring."

Fish or Protein Bait (No Insecticide) Traps

Various traps using fish or other meat baits have been constructed to collect workers of scavenging species of yellowjackets. While shape and size of these traps vary, nearly all use a reverse screen cone so workers can readily enter the trap but cannot find their way back out. Disadvantages of using the trap include (1) keeping the bait fresh (yellowjackets will not scavenge spoiled flesh) by replacing it every other day, and (2) killing and removing all collected workers.

Fish/Wetting Agent/Water Traps

One of the oldest and still effective control methods for yellowjacket workers involves suspending a raw fish several centimeters above a pan filled with water to which a wetting agent has been added (fig. 73). The skin on the sides of the fish should be broken or cut to give ready access to the flesh.

Typical worker behavior is to cut a piece of flesh from the carcass, then to fly a short distance where it alights to trim the piece to a manageable size. The initial piece is frequently so heavy the worker has difficulty flying and drops toward the substrate. Thus, when flying from the fish bait, many workers fall into the water, and since the surface film has been reduced by the wetting agent, they sink and drown.

During the outbreak of yellowjackets in the Pacific Northwest in 1973, *V. pensylvanica* workers were extremely abundant at a resort at

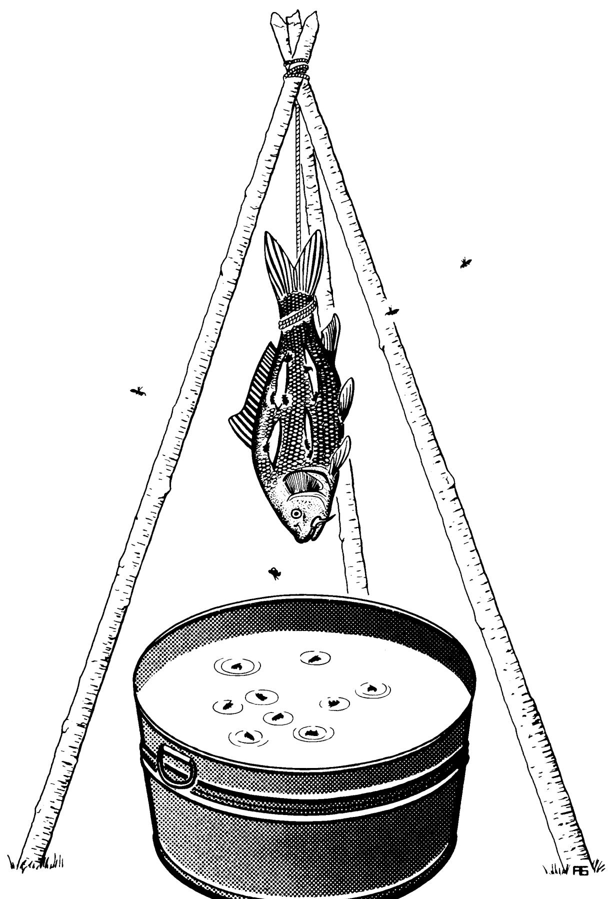


FIGURE 73 — Raw fish, with sides cut to expose flesh, suspended above a pan of water to which a wetting agent has been added. Yellowjacket workers attempt to fly away with a large piece of flesh, fall into the water, and drown.

Loon Lake, Wash., causing many guests to cancel reservations or curtail their activities. Nine fish traps were placed at various locations around the resort, and within one week nearly 1,000 yellowjacket workers were captured. Continued use of these traps in combination with several other control procedures reduced, within 2 weeks, the number of workers flying in the area to a level that guests would tolerate.

Since these traps are easily constructed, use no toxic materials, and are specific for scavenger species, this method of reducing yellowjacket populations in specific areas remains one of the best. Two serious disadvantages of this method are the unavailability of rough fish to use as bait, and removal of fish from traps by dogs or cats; however, if the latter is a serious problem, a chicken wire or hardware cloth cage can be placed around the trap.

Repellent Jackets

Several commercial manufacturers produce jackets impregnated with chemicals repellent to biting flies. These jackets are of no value in repelling yellowjackets.

Control Summary

1. Yellowjackets, including scavenger species, should not be controlled or eliminated unless they are pestiferous because all yellowjackets are beneficial.
2. All colonies should be exterminated at night when the workers are least active and the maximum number are within the nest.
3. Subterranean colonies can be eliminated with the use of insecticides such as carbaryl or propoxur. These insecticides are poured into the entrance tunnel which is then plugged with cotton. The plug and surrounding soil should also be treated to kill any foragers returning the next day. Certain aerosols will also effectively control colonies if the nest is near the entrance hole.
4. Colonies in wall voids are effectively controlled by use of a synthetic pyrethroid generator and application of carbaryl dust to the plugged entrance hole.
5. Aerial nests can be easily treated with aerosol products containing a quick knockdown insecticide. Several types of commercial products

will propel a thin stream of insecticide and solvent up to 3 m or more. Aerial nests may also be sprayed with conventional insecticides such as propoxur.

6. Simple traps using a fish as bait with a pan beneath containing water and a wetting agent can be quite effective in lowering populations of yellowjackets in small areas. These traps have the advantage of being specific for scavenging species. Other traps using fish as bait and a reverse cone to trap entering workers are effective but not as convenient as other methods.

7. At the present time, poison bait formulations are effective only against *V. pensylvanica* and, to a lesser extent, against *V. vulgaris*. The only effective programs utilizing this technique were in California. More research is needed to discover acceptable baits for pestiferous species in other areas.

8. Synthetic lure traps containing heptyl butyrate or other attractants have been used effectively to abate populations of *V. pensylvanica* in some arid areas of Washington and Oregon. In most areas of North America, these lures have no value as most species are not attracted. Hopefully, future research will uncover additional compounds that are differentially attractive to some of the other species. This type of trapping is not recommended for homeowners.

9. One of the best methods of reducing contact with yellowjackets (and perhaps even reducing populations) in urban areas is to control garbage by making it less available to scavenging workers. Treatment of trash containers routinely with dichlorvos sprays or placing an insecticide impregnated strip in the garbage can lid also helps.

ACKNOWLEDGMENTS

It is impossible to write a handbook of this scope without the help and cooperation of a large number of scientists who gave freely of their data, their photographs, and their time. Without their help, many sections of this publication would be much less informative. While this small note cannot begin to express our real appreciation, we extend it as a grateful thank you.

We thank the following for the loan of yellowjacket specimens: J.D. Lattin and G. Ferguson, Department of Entomology, Oregon State University, Corvallis; R.H. Washburn, USDA, Palmer, Alaska; T.J. Zavortink, California Academy of Science, San Francisco; P.J. Hurd, Smithsonian Institution, Washington, D.C.; A.S. Menke, Systematic Entomology Laboratory, U.S. National Museum, Washington, D.C.; M. Favreau, American Museum of Natural History, New York City; H.V. Daly, Division of Entomology and Parasitology, University of California, Berkeley; and W.J. Turner, M.T. James Entomological Collection, Washington State University, Pullman.

Appreciation is extended to the following researchers who permitted us to cite their unpublished data or observations: C.W. Rettenmeyer, Biological Sciences Group, University of Connecticut, Storrs; C.F. Roush, Department of Entomology, Washington State University, Pullman; R. Keyel, Department of Entomology, Cornell University, Ithaca, N.Y.; J. Nixon, Allied Exterminating Services, Silver Spring, Md.; R.E. Wagner, Department of Entomology, University of California, Riverside; R.W. Matthews, Department of Entomology, University of Georgia, Athens; J. Sharp, Insect Attractants and Basic Biology Laboratory, USDA, Gainesville, Fla.; C.A. Johansen, Department of Entomology, Washington State University, Pullman; F. Ennik, California Department of Health, Berkeley; R.W. Zwick, Oregon State University Experiment Station, Hood River; and W.B. Robinson, Department of Food Science and Technology, Cornell University, Ithaca, N.Y.

J. Schuh, Klamath Falls, Oreg., A.A. Antonelli, Western Washington Experiment and Extension Center, Puyallup, and W. Baker, Friday Harbor, Wash., are acknowledged for the many yellowjacket specimens and nests they presented to us during the course of conducting the research that led to this handbook.

Photographs used in illustrating some of the text were obtained from: C.W. Rettenmeyer; R. Keyel; J. Nixon; C.F. Roush; R. Oetting, Department of Entomology, Georgia Agricultural

Experiment Station, Experiment, Ga.; and W.D. Lord, Department of Entomology, University of Delaware, Newark.

Special thanks are due to J. Nixon for his critical reading of sections of the manuscript and in advice with chemical control, to C.F. Roush for his criticism of parts of the manuscript and for his many helpful assistances, and to D.M. Jackson, Department of Entomology, Washington State University, Pullman, for his untiring help with data, illustrations, collating materials, and checking literature.

Several illustrations used in this publication were prepared by G. Shinn, University of Washington, Seattle, and S. Peck, Washington State University. Joan Krispyn, Department of Entomology, University of Georgia, Athens, drew the illustrations of the *Polistes* nest and the yellowjacket life cycle. All other illustrations are by Al Greene. Photographs not credited to other personnel were taken by the authors.

Much of the information contained in the handbook was obtained from research projects at Washington State University, funded by National Science Foundation (grants GB-30922 and BNS 76-81400), the USDA, Science and Education Administration (cooperative agreement), and the USDA, Douglas-fir Tussock Moth Expanded Research and Development Program (CSRS grant 704-15-16); from projects at the University of Georgia, Department of Entomology; and from Purdue University Experiment Station project 58045.

LITERATURE CITED

AKRE, R. D., AND A. H. RETAN.
1973. YELLOWJACKETS AND PAPER WASPS. Wash. State Univ. Ext. Bul. 653, 4 pp.

_____ J. F. MACDONALD, AND W. B. HILL.
1974. YELLOWJACKET LITERATURE (HYMENOPTERA: VESPIDAE). Melanderia 18:67–93.

_____ W. B. HILL, J. F. MACDONALD, AND W. B. GARNETT.
1975. FORAGING DISTANCE OF *VESPULA PENSYLVANICA* WORKERS (HYMENOPTERA: VESPIDAE). Kans. Ent. Soc. J. 48: 12–16.

_____ W. B. GARNETT, J. F. MACDONALD, AND OTHERS.
1976. BEHAVIOR AND COLONY DEVELOPMENT OF *VESPULA PENSYLVANICA* AND *VESPULA ATROPILOSA* NEST (HYMENOPTERA: VESPIDAE). Kans. Ent. Soc. J. 49:63–84.

_____ AND H. G. DAVIS.
1978. BIOLOGY AND PEST-STATUS OF VENOMOUS WASPS. Ann. Rev. Ent. 23:215–238.

_____ C. F. ROUSH, AND P. J. LANDOLT.
1977. A *VESPULA PENSYLVANICA/VESPULA VULGARIS* NEST (HYMENOPTERA: VESPIDAE). Environ. Ent. 6:525–526.

ARCHER, M. E.
1972a. STUDIES OF THE SEASONAL DEVELOPMENT OF *VESPULA VULGARIS* WITH SPECIAL REFERENCE TO QUEEN PRODUCTION. J. Ent. (A) 47:45–59.

_____
1972b. THE IMPORTANCE OF WORKER BEHAVIOR IN THE COLONY ORGANIZATION OF THE SOCIAL WASPS, *VESPULA VULGARIS* (L.) AND *V. GERMANICA* (F.) (VESPIDAE: HYMENOPTERA). Insectes Soc. 19:227–242.

_____
1972c. THE SIGNIFICANCE OF WORKER SIZE IN THE SEASONAL DEVELOPMENT OF THE WASPS *VESPULA VULGARIS* (L.) AND *VESPULA GERMANICA* (F.). J. Ent. (A) 46: 175–183.

_____
1973. THE POPULATION ECOLOGY OF *VESPULA VULGARIS* (L.), (VESPIDAE: HYMENOPTERA) AND THE COMPUTER SIMULATION OF COLONIAL SEASONAL DEVELOPMENT. International Union for the Study of Social Insects (IUSSI) Proc. VII Internatl. Congress, pp. 2–10.

_____
1977a. TREE WASP WORKERS (HYMENOPTERA: VESPIDAE) EXCAVATING SOIL FROM UNDERGROUND NESTS. Ent. Mon. Mag. 112:88.

_____
1977b. THE WEIGHTS OF FORAGER LOADS OF *PARAVESPULA VULGARIS* (LINN.) (HYMENOPTERA: VESPIDAE) AND THE RELATIONSHIP OF LOAD WEIGHT TO FORAGER SIZE. Insectes Soc. 24:95–102.

BALDUF, W. V.
1954. OBSERVATIONS ON THE WHITE-FACED WASP *DOLICHOVESPULA MACULATA* (LINN) (VESPIDAE, HYMENOPTERA). Ann. Ent. Soc. Amer. 47:445–458.

_____
1968a. ON THE LIFE OF *VESPULA VULGARIS* (L.) AND *V. MACULIFRONS* (BUYSSON) (HYMENOPTERA: VESPIDAE). Ent. Soc. Wash. Proc. 70:332–338.

_____
1968b. ON THE FLIGHT BEHAVIOR OF WORKER *VESPULA MACULIFRONS* (BUYSSON) (HYMENOPTERA: VESPIDAE). Illinois Acad. Sci. Trans. 61:400–406.

BARNARD, J. H.
1973. STUDIES OF 400 HYMENOPTERA STING DEATHS IN THE UNITED STATES. Allergy Clin. Immun. J. 52:259–264.

BARR, S. E.
1971. ALLERGY TO HYMENOPTERA STINGS. Review of the world literature: 1953–1970. Ann. Allergy 29:49–66.

BEAMER, R. H.
1925. THE OVERWINTERING OF *VESPULA COMMUNIS* VAR. *FLAVIDA* SLADEN (HYMENOPTERA: VESPIDAE). Ent. News 36:309–310.

BENTON, A. W. AND R. A. HECKMAN.
1969. FACTS CONCERNING STINGING INSECTS, THEIR VENOMS, AND HUMAN REACTIONS TO STINGS. Amer. Bee J. 109:222–223, 262–263.

BEQUAERT, J.
1918. A REVISION OF THE VESPIDAE OF THE BELGIAN CONGO BASED ON THE COLLECTION OF THE AMERICAN MUSEUM CONGO EXPEDITION, WITH A LIST OF ETHIOPIAN DIPLOPTEROUS WASPS. Amer. Mus. Nat. Hist. Bul. 39:1–384.

_____
1931. A TENTATIVE SYNOPSIS OF THE HORNETS AND YELLOW-JACKETS (VESPINAE: HYMENOPTERA) OF AMERICA. Ent. Amer. 12:71–138.

_____
1933. THE NEARCTIC SOCIAL WASPS OF THE SUBFAMILY POLYBIINAE (HYMENOPTERA: VESPIDAE). Ent. Amer. 13:87–150.

BOHART, R. M. AND R. C. BECHTEL.
1957. THE SOCIAL WASPS OF CALIFORNIA (VESPINAE, POLISTINAE, POLYBIINAE). Calif. Insect Surv. Bul. 4:73–101.

BRADLEY, J. C.
1922. THE TAXONOMY OF THE MASARID WASPS, INCLUDING A MONOGRAPH ON THE NORTH AMERICAN SPECIES. Univ. Calif. Tech. Bul. 1:369–464.

BROTHERS, D. J.
1975. PHYLOGENY AND CLASSIFICATION OF THE ACULEATE HYMENOPTERA, WITH SPECIAL REFERENCE TO MUTILLIDAE. Univ. Kans. Sci. Bul. 50:483–648.

BUCKELL, E. R., AND G. J. SPENCER.
1950. THE SOCIAL WASPS (VESPIDAE) OF BRITISH COLUMBIA. Ent. Soc. Brit. Columbia Proc. 46:33–40.

BURKANTZ, S. C.
1975. DEATHS FOLLOWING INSECT STINGS. Hosp. Pract. 10:12–13.

CARPENTER, G. H., AND D. R. PACK-BERESFORD.
1903. THE RELATIONSHIP OF *VESPA AUSTRIACA* TO *VESPA RUFA*. Ent. Mon. Mag. 39:230–242.

CORBETT, J. E.
1966. THE TEMPLE TIGER AND MORE MAN-EATERS OF KUMAON. Oxford University Press, New York. 197 pp.

DAVIS, H. G.
1978. YELLOWJACKET WASPS IN URBAN ENVIRONMENTS. *In* Frankie, G. W. and C. S. Koehler, eds., Perspectives in Urban Entomology, Chapt. 7, pp. 163–185. Internatl. Congress Ent. Academic, New York. 417 pp.

_____ G. W. EDDY, T. P. MCGOVERN, AND M. BEROZA.
1967. 2-4-HEXADIENYL BUTYRATE AND RELATED COMPOUNDS HIGHLY ATTRACTIVE TO YELLOWJACKETS (*VESPULA* SPP.). Med. Ent. J. 4:275–280.

_____ R. W. ZWICK, W. M. ROGOFF, AND OTHERS.
1973. PERIMETER TRAPS BAITED WITH SYNTHETIC LURES FOR SUPPRESSION OF YELLOWJACKETS IN FRUIT ORCHARDS. Environ. Ent. 2:569–571.

DOW, R.
1930. THE NESTS OF NEW ENGLAND WASPS. Boston Soc. Nat. Hist. Bul. 56:11–16.

DUNCAN, C. D.
1939. A CONTRIBUTION TO THE BIOLOGY OF NORTH AMERICAN VESPINE WASPS. Stanford Univ. Pub. Biol. Sci. 8:1–282.

EBELING, W.
1975. SOCIAL WASPS (VESPIDAE) pp. 353-364, *In* Urban Entomology, Univ. Calif. Div. Agric. Sci., Berkeley. 695 pp.

EDWARDS, R.
1976. THE WORLD DISTRIBUTION PATTERN OF THE GERMAN WASP, *PARAVESPULA GERMANICA* (HYMENOPTERA: VESPIDAE). Ent. Germanica 3:269–271.

ENNICK, F.
1973. ABATEMENT OF YELLOWJACKETS USING ENCAPSULATED FORMULATIONS OF DIAZINON AND RABON. J. Econ. Ent. 66:1097–1098.

EVANS, H. E.
1975. SOCIAL PARASITISM OF A COMMON YELLOWJACKET. Insect World Dig. 2(1):6–13.

_____ AND M. J. W. EBERHARD.
1970. THE WASPS. University of Michigan Press, Ann Arbor. 265 pp.

FEINGOLD, B. F.
1973. INTRODUCTION TO CLINICAL ALLERGY. C. C. Thomas, Springfield, Ill. 380 pp.

FERRO, D. N., ED.
1976. NEW ZEALAND INSECT PESTS. Lincoln Univ. Col. Agric., Canterbury. 311 pp.

FLUNO, J. A.
1961. WASPS AS ENEMIES OF MAN. Ent. Soc. Amer. Bull. 7:117–119.

_____
1973. CHEMICAL PROOF OF THE VALIDITY OF THE TAXONOMIC SEPARATION OF *VESPULA* SUBGENUS *VESPULA* FROM *VESPULA* SUBGENUS *DOLICHOVESPULA*. Ent. Soc. Wash. Proc. 75:80–83.

FRAZIER, C. A.
1976. INSECT STINGS—A MEDICAL EMERGENCY. Amer. Med. Assoc. J. 235:2410–2411.

FREE, J. B.
1970. THE BEHAVIOR OF WASPS (*VESPULA GERMANICA* L. AND *V. VULGARIS* L.) WHEN FORAGING. Insectes Soc. 17:11–20.

GAUL, A. T.
1948. ADDITIONS TO VESPINE BIOLOGY. VI. NOTES ON *VESPULA RUFA* VAR. *CONSOBRINA* SAUSSURE. Brooklyn Ent. Soc. Bul. 43:160–162.

_____
1952. ADDITIONS TO VESPINE BIOLOGY. X. FORAGING AND CHEMOTAXIS. Brooklyn Ent. Soc. Bul. 47:138–140.

GELLER, R. G., H. YOSHIDA, M. A. BEAVEN, AND OTHERS.
1976. PHARMACOLOGICALLY ACTIVE SUBSTANCES IN VENOMS OF THE BALDFACED HORNET, *VESPULA (DOLICHOVESPULA) MACULATA* AND THE YELLOWJACKET, *VESPULA (VESPULA) MACULIFRONS.* Toxicon 14:27–33.

GIBO, D. L., R. M. YARASCAVITCH, AND H. E. DEW.
1974a. THERMOREGULATION IN COLONIES OF *VESPULA ARENARIA* AND *VESPULA MACULATA* (HYMENOPTERA: VESPIDAE) UNDER NORMAL CONDITIONS AND UNDER COLD STRESS. Can. Ent. 106:503–507.

——— H. E. DEW, AND A. S. HAJDUK.
1974b. THERMOREGULATION IN COLONIES OF *VESPULA ARENARIA* AND *VESPULA MACULATA* (HYMENOPTERA: VESPIDAE) II. THE RELATION BETWEEN COLONY BIOMASS AND CALORIE PRODUCTION. Can. Ent. 106: 873–879.

——— A. TEMPORALE, T. P. LAMARRE, AND OTHERS.
1977. THERMOREGULATION IN COLONIES OF *VESPULA ARENARIA* AND *VESPULA MACULATA* (HYMENOPTERA: VESPIDAE) III. HEAT PRODUCTION IN QUEEN NESTS. Can. Ent. 109:615–620.

GRANT, J.
1959. HUMMINGBIRDS ATTACKED BY WASPS. Can. Field Nat. 73:174.

GRANT, C. D.
1963. NEEDS AND POTENTIALS FOR YELLOWJACKET CONTROL. Calif. Mosq. Control Assoc. Proc. 31:41–44.

——— C. J. ROGERS, AND T. H. LAURET.
1968. CONTROL OF GROUND-NESTING YELLOWJACKETS WITH TOXIC BAITS—A FIVE YEAR PROGRAM. J. Econ. Ent. 61:1653–1656.

GREEN, S. G., R. A. HECKMAN, A. W. BENTON, AND B. F. COON.
1970. AN UNUSUAL NEST LOCATION FOR *VESPULA MACULIFRONS* (HYMENOPTERA: VESPIDAE). Ann. Ent. Soc. Amer. 63:1197–1198.

GREENE, A., R. D. AKRE, AND P. J. LANDOLT.
1976. THE AERIAL YELLOWJACKET, *DOLICHOVESPULA ARENARIA* (FAB.): NESTING BIOLOGY, REPRODUCTIVE PRODUCTION, AND BEHAVIOR (HYMENOPTERA: VESPIDAE). Melanderia 26:1–34.

——— R. D. AKRE, AND P. J. LANDOLT.
1978. BEHAVIOR OF THE YELLOWJACKET SOCIAL PARASITE, *DOLICHOVESPULA ARCTICA* (ROHWER) (HYMENOPTERA: VESPIDAE). Melanderia 29:1–28.

GROTHAUS, R. H., H. G. DAVIS, W. M. ROGOFF, AND OTHERS.
1973. BAITS AND ATTRACTANTS FOR EAST COAST YELLOWJACKETS, *VESPULA* SPP. Environ. Ent. 2:717–718.

GUIGLIA, D.
1972. LES GUÊPES SOCIALES (HYMENOPTERA: VESPIDAE) D'EUROPE OCCIDENTALE AT SEPTENTRIONALE. FAUNE DE L'EUROPE ET DU BASSIN MÉDITERRANÉEN. Masson, Paris. 6:1-181.

HABERMANN, E.
1972. BEE AND WASP VENOMS. Science 177:314–322.

HAVILAND, E. E.
1962. OBSERVATIONS ON THE STRUCT RE AND CON ENTS YELLOWJACKET NESTS (HYMEN PTERA). Ent. Soc. Wash. Proc. 64:181–183.

HITCHCOCK, S. W.
1970. WASPS IN CONNECTICUT: APPEARANCE, HABITS, CONTROL. Conn. Agric. Exp. Stn. Cir. 236.

HOWARTH, F. G.
1975. REPORTS OF *VESPULA VULGARIS* ON MAUI, HAWAII. Hawaiian Ent. Soc. Proc. 22:11–12.

HOWELL, J. F., AND H. G. DAVIS.
1972. PROTECTING CODLING MOTHS CAPTURED IN SEX-ATTRACTANT TRAPS FROM PREDACEOUS YELLOWJACKETS.. Environ. Ent. 1:122–123.

HOWELL, J. O.
1973. NOTES ON YELLOWJACKETS AS A FOOD SOURCE FOR THE BALD FACED HORNET, *VESPULA MACULATA* (L.). Ent. News 84:141–142.

——— T. P. MCGOVERN, AND M. BEROZA.
1974. ATTRACTIVENESS OF SYNTHETIC COMPOUNDS TO SOME EASTERN *VESPULA* SPECIES. J. Econ. Ent. 67:629-630.

HUNT, K. J., M. D. VALENTINE, A. K. SOBOTKA, AND OTHERS.
1978. A CONTROLLED TRIAL OF IMMUNOTHERAPY IN INSECT HYPERSENSITIVITY. NEW ENGLAND J. MED 299: 157-161.

HURD, P. D.
1955. THE ACULEATE WASPS. pp. 573–575. *In* Kessel, E.L., ed., A Century of Progress in the Natural Sciences, 1853-1953. Calif. Acad. Sci., San Francisco. 807 pp.

ISHAY, J., AND M. B. BROWN.
1975. PATTERNS IN THE SOUNDS PRODUCED BY *PARAVESPULA GERMANICA* WASPS. Acoust. Soc. Amer. J. 57:1521–1525.

IWATA, K.
1976. EVOLUTION OF INSTINCT: COMPARATIVE ETHOLOGY OF HYMENOPTERA. Amerind, New Delhi. 535 pp.

JACOBSON, R. S., R. W. MATTHEWS, AND J. F. MACDONALD.
1978. A SYSTEMATIC STUDY OF THE *VESPULA VULGARIS* GROUP WITH A DESCRIPTION OF A NEW YELLOWJACKET SPECIES IN EASTERN NORTH AMERICA (HYMENOPTERA: VESPIDAE). Ann. Ent. Soc. Amer. 71:299–311.

JANET, C.
1895. ÉTUDES SUR LES FOURMIS, LES GUÊPES ET LES ABEILLES. NEUVIEME NOTE. SUR *VÊSPA CRABRO* L. HISTOIRE D'UN NID DEPUIS SON ORIGINE. Mém. Soc. Zool. France 8:1–141.

———
1903. OBSERVATIONS SUR LES GUÊPES. C. Naud, Paris. 85 pp.

JEANNE, R. L.
1977. BEHAVIOR OF THE OBLIGATE SOCIAL PARASITE *VESPULA ARCTICA* (HYMENOPTERA: VESPIDAE). Kans. Ent. Soc. J. 50:541–557.

KEH, B., N. T. BROWNFIELD, AND M. E. PERSONS.
1968. EXPERIMENTAL USE OF BAIT WITH MIREX LETHAL TO BOTH ADULT AND IMMATURE *VESPULA PENSYLVANICA* (HYMENOPTERA: VESPIDAE). Calif. Vector Views 15:115–118.

KEMPER, H.
1961. NESTUNTERSCHIEDE BEI DEN SOZIALEN FALTENWESPEN DEUTSCHLANDS. Zeit. Angew. Zool. 48: 31–85.

_____ AND E. DÖHRING.
1967. DIE SOZIALEN FALTENWESPEN MITTELEUROPAS. Paul Parey, Berlin. 180 pp.

KUGLER, J., T. ORION, AND J. ISHAY.
1976. THE NUMBER OF OVARIOLES IN THE VESPINAE (HYMENOPTERA). Insectes Soc. 23:525-533.

KULHORN, F.
1961. ÜBER DAS VERHALTEN SOZIALEN FALTENWESPEN (HYMENOPTERA: VESPIDAE) BEIM STALLEINFLUG, INNERHALB VON VEIHSTÄLLEN AND BEIM FLIEGANFANG. Zeit. Angew. Zool. 48:405-422.

KURCZEWSKI, F. E.
1968. *VESPULA MACULIFRONS* (HYMENOPTERA: VESPIDAE) PREYING ON THE EUROPEAN EARWIG *FORFICULA AURICULARIA*. N.Y. Ent. Soc. J. 76:84–86.

LECLERCQ, M., AND J. LECOMTE.
1975. SUR LES ACCIDENTS GRAVES PROVOQÚES PAR LES PIQÛRES D'HYMÉNOPTÈRES ACULÉATES. Spectrum 18:1–14.

LECOMTE, J., AND M. LECLERCQ.
1973. SUR LA MORT PROVOQUÉE PAR LES PIQÛRES D'HYMÉNOPTÈRES ACULÉATES. Acad. Med. Belg. Bul. 128: 615–693.

LICHTENSTEIN, L. M.
1975. ANAPHYLACTIC REACTIONS TO INSECT STINGS: A NEW APPROACH. Hosp. Pract. 10:67–74.

LØKEN A.
1964. SOCIAL WASPS IN NORWAY (HYMENOPTERA: VESPIDAE). Norsk Ent. Tidsskr. 12: 195–218.

_____
1965. A NEST OF *VESPULA SAXONICA* (FABR.) (HYM., VESPIDAE). Norsk Ent. Tidsskr. 13:36–40.

MACDONALD, J. F., R. D. AKRE, AND W. B. HILL.
1973. ATTRACTION OF YELLOWJACKETS (*VESPULA* SPP.) TO HEPTYL BUTYRATE IN WASHINGTON STATE (HYMENOPTERA: VESPIDAE). Environ. Ent. 2:375–379.

_____ R. D. AKRE, AND W. B. HILL.
1975b. COMPARATIVE BIOLOGY AND BEHAVIOR OF *VESPULA ATROPILOSA* AND *V. PENSYLVANICA* (HYMENOPTERA: VESPIDAE). Melanderia 18:1–66.

_____ R. D. AKRE, AND W. B. HILL.
1975a. LOCATIONS AND STRUCTURE OF NESTS OF *VESPULA ATROPILOSA* AND *V. ACADICA* (HYMENOPTERA: VESPIDAE). Kans. Ent. Soc. J. 48:114–121.

_____ R. D. AKRE, AND W. B. HILL
1972b. NEST ASSOCIATES OF *VESPULA ATROPILOSA* AND *V. PENSYLVANICA* IN SOUTHEASTERN WASHINGTON STATE (HYMENOPTERA: VESPIDAE). Kans. Ent. Soc. J. 48:53–63.

_____ R. D. AKRE, AND R. W. MATTHEWS.
1976. EVALUATION OF YELLOWJACKET ABATEMENT IN THE UNITED STATES. Ent. Soc. Amer. Bul. 22: 397–401.

_____ AND R. W. MATTHEWS.
1975. *VESPULA SQUAMOSA*: A YELLOWJACKET WASP EVOLVING TOWARD PARASITISM. Science 190:1003–1004.

_____ AND R. W. MATTHEWS.
1976. NEST STRUCTURE AND COLONY COMPOSITION OF *VESPULA VIDUA* AND *V. CONSOBRINA* (HYMENOPTERA: VESPIDAE). Ann. Ent. Soc. Amer. 69:471–475.

_____ AND R. W. MATTHEWS.
198_a. NESTING BIOLOGY OF THE EASTERN YELLOWJACKET, *VESPULA MACULIFRONS* (HYMENOPTERA: VESPIDAE). (In preparation.)

_____ AND R. W. MATTHEWS.
198_b. NESTING BIOLOGY OF THE SOUTHERN YELLOWJACKET, *VESPULA SQUAMOSA* (HYMENOPTERA: VESPIDAE). (In press.) Ann. Ent. Soc. Amer.).

_____ R. W. MATTHEWS, AND R. S. JACOBSON
1980. COMPARATIVE NESTING BIOLOGY OF THE YELLOWJACKET, *VESPULA FLAVOPILOSA*, (HYMENOPTERA: VESPIDAE). J. Kans. Ent. Soc. 53 (In press).

MASCHWITZ, U. W. J., AND W. KLOFT.
1971. MORPHOLOGY AND FUNCTION OF THE VENOM APPARATUS OF INSECTS-BEES, WASPS, ANTS, AND CATERPILLARS. Chapt. 44:1–60. *In* Bucherl, W., and E. Buckley, eds., Venomous Animals and Their Venoms, vol. III, Venomous Invertebrates. Academic Press, New York. 537 pp.

MATSUURA, M.
1968. LIFE OF HORNETS. PART II. ROYAL COURT AROUND QUEENS OF *VESPA* SPECIES. (*In* Japanese). Japanese Bee J. 21:21–25. Cited by Spradbery, J. P. 1973a. WASPS. AN ACCOUNT OF THE BIOLOGY AND NATURAL HISTORY OF SOLITARY AND SOCIAL WASPS. University of Washington Press, Seattle. 408 pp.

_____
1969. BEHAVIOR OF POST-HIBERNATING FEMALE HORNETS *VESPA*, IN THE PRENESTING STAGE, WITH SPECIAL REFERENCE TO INTRA- AND INTERSPECIFIC DOMINANCE RELATIONSHIPS. Japanese J. Ecol. 19:196–203.

_____
1970. INTRASPECIFIC INVASION BEHAVIOUR OF *VESPA CRABRO FLAVOFASCIATA* CAMERON IN EARLY STAGE OF NESTING. Life Study (Fukui) 14:21–26.

_____
1971. NEST FOUNDATION BY THE FEMALE WASPS OF THE GENUS *VESPA* (HYMENOPTERA, VESPIDAE). Kontyû 39:99–105.

_____
1973. COLONY DEVELOPMENT OF *VESPA CRABRO FLAVOFASCIATA* CAMERON IN EARLY STAGE OF NESTING. Life Study (Fukui) 12:1–12.

_____
1974. INTRACOLONIAL POLYETHISM IN *VESPA*. BEHAVIOUR AND ITS CHANGE OF THE FOUNDRESS OF *VESPA CRABRO FLAVOFASCIATA* IN EARLY NESTING STAGE IN RELATION TO WORKER EMERGENCE. Kontyu 42:333–350.

_____ AND S. F. SAKAGAMI.
1973. A BIONOMIC SKETCH OF THE GIANT HORNET, *VESPA MANDARINIA*, A SERIOUS PEST FOR JAPANESE AGRICULTURE. Fac. Sci. Hokkaido Univ. J. Series VI Zool. 19:125–162.

MENKE, A. S., AND R. SNELLING.
1975 *VESPULA GERMANICA* (FABRICIUS), AN ADVENTIVE YELLOW JACKET IN THE NORTHEASTERN UNITED STATES (HYMENOPTERA: VESPIDAE). U.S. Dept. Agric. Coop. Econ. Insect Rept. 25:193–200.

MILLER, C. D. F.
1958. DISTRIBUTION AND NOMENCLATORIAL PROBLEMS IN SOME FORMS OF *VESPULA* IN NORTH AMERICA. 10th International Congress Ent. Proc. 1:257–264.
——— 1961. TAXONOMY AND DISTRIBUTION OF NEARCTIC *VESPULA*. Can. Ent. Suppl. 22:1–52.

MONTAGNER, H.
1966. LE MÉCHANISME ET LES CONSÉQUENCES DES COMPORTEMENTS TROPHALLACTIQUES CHEZ LES GUÊPES DU GENRE *VESPA*. THÈSES DE L'UNIVERSITE DE NANCY. Periquenx. 143 pp.

MORRIS, R. F.
1972. PREDATION BY WASPS, BIRDS, AND MAMMALS ON *HYPHANTRIA CUNEA*. Can. Ent. 104:1581–1591.

MORSE, R. A., G. C. EICKWORT, AND R. S. JACOBSON.
1977. THE ECONOMIC STATUS OF AN IMMIGRANT YELLOWJACKET, *VESPULA GERMANICA* (HYMENOPTERA: VESPIDAE), IN NORTHEASTERN UNITED STATES. Environ. Ent. 6:109–110.

NIXON, G. E. J.
1935. NOTES ON WASPS. IV. Ent. Mon. Mag. 71:106–111.

NOWAK, G.
1972. ALLERGY TO ARTHROPOD STINGS. LIT. SEARCH JAN. 1969 THROUGH NOV. 1972. Natl. Libr. Med., Lit. Search No. 72–37, 6 pp.

O'CONNER, R., AND R. ERICKSON.
1965. HYMENOPTERA ANTIGENS: AN IMMUNOLOGICAL COMPARISON OF VENOMS, VENOM SAC EXTRACTS AND WHOLE INSECT EXTRACTS. Ann. Allergy 23:151–157.

PACK-BERESFORD, D. R.
1904. ANOTHER NEST OF *VESPA RUFA-AUSTRIACA*. Irish Nat. 13:242.

PARDI, L.
1948. DOMINANCE ORDER IN *POLISTES* WASPS. Physiol. Zool. 21:1–13.

PARRISH, H. M.
1959. DEATHS FROM BITES AND STINGS OF VENOMOUS ANIMALS AND INSECTS IN THE UNITED STATES. Arch. Intern. Med.104:198–207.
——— 1963. ANALYSIS OF 460 FATALITIES FROM VENOMOUS ANIMALS IN THE UNITED STATES. Amer. J. Med. Sci. 256:129–141.

PAYNE, J. A., AND W. R. M. MASON.
1971. HYMENOPTERA ASSOCIATED WITH PIG CARRION. Ent. Soc. Wash. Proc. 73:132–141.

PEÑA, G., L. E., R. PÉREZ DE ARCE, AND L. CARTAGENA C.
1975. LA PRESENCIA DE *VESPULA MACULIFORNS* (BUYSSON), (HYMENOPTERA: VESPIDAE) EN CHILE. [= *VESPULA GERMANICA*]. Rev. Chilena Ent. 9:167–168.

PERLMAN, F.
1962. INSECTS AS ALLERGEN INJECTANTS. Calif. Med. 96:1–10.

PERROTT, D. C. F.
1975. FACTORS AFFECTING USE OF MIREX-POISONED PROTEIN BAITS FOR CONTROL OF EUROPEAN WASP *(ParaVESPULA GERMANICA)* IN NEW ZEALAND. New Zealand J. Zool. 2:491-508.

POINAR, G. O., AND F. ENNICK.
1972. THE USE OF *NEOAPLECTANA CARPOCAPSAE* (STEINERNEMATIDAE: RHABDITOIDEA) AGAINST ADULT YELLOWJACKETS (*VESPULA* SPP., VESPIDAE: HYMENOPTERA). J. Invert. Path. 19:331–334.

PUTMAN, S. E., JR.
1977. CONTROLLING STINGING AND BITING INSECTS AT CAMPSITES. Project Record, ED & T 2689. Control of stinging insects in Forest Service Camps. U.S. Dept. Agric., Forest Service Equip. Dev. Center, Missoula, Mont. 22 pp.

RAU, P.
1929. THE NESTING HABITS OF THE BALD-FACED HORNET, *VESPA MACULATA*. Ann. Ent. Soc. Amer. 22:659–675.

REED, H. C., R. D. AKRE, AND W. B. GARNETT.
1979. A NORTH AMERICAN HOST OF THE YELLOWJACKET SOCIAL PARASITE *VESPULA AUSTRIACA* (PANZER) (HYMENOPTERA: VESPIDAE). Ent. News 90:110–113.

REISMAN, R. E.
1975. INSECT STINGS—DANGER SEASON OPENS. U.S. News & World Report 78(16):65.

RICHARDS, O. W.
1962. A REVISIONAL STUDY OF THE MASARID WASPS (HYMENOPTERA: VESPOIDEA). British Museum (Natural History), London. 294 pp.
——— 1978. THE SOCIAL WASPS OF THE AMERICAS EXCLUDING THE VESPINAE. British Museum (Natural History), London. 580 pp.

ROGERS, C. J.
1972. FIELD TESTING OF "YELLOWJACKET STOPPERS" AND POPULATION DEPLETION TRAPPING FOR THE CONTROL OF GROUND-NESTING YELLOWJACKETS. Calif. Mosq. Cont. Assoc. Proc. 40:132–134.

ROUSH, C. F., AND R. D. AKRE.
1978. NESTING BIOLOGIES AND SEASONAL OCCURRENCE OF YELLOWJACKETS IN NORTHEASTERN OREGON FORESTS (HYMENOPTERA: VESPIDAE). Melanderia 30:57–94.

SCHMIDTMANN, E. T.
1977. MUSCID FLY PREDATION BY *VESPULA GERMANICA* (HYMENOPTERA: VESPIDAE). Environ. Ent. 6:107–108.

SHARP, D.
1903. *VESPA RUFA* + *AUSTRIACA*. Ent. Mon. Mag. 14: 297–299.

SHAW, F. R., AND J. WEIDHAAS, JR.
1956. DISTRIBUTION AND HABITS OF THE GIANT HORNET IN NORTH AMERICA. J. Econ. Ent. 49:275.

SIMON, R. P., AND A. W. BENTON.
1968. WINTER ACTIVITIES OF *VESPULA MACULIFRONS*. Ann. Ent. Soc. Amer. 61:542–544.

SLADEN, F. W. L.
1918. THE GENUS *VESPA* IN CANADA. Ottawa Nat. 22: 71–72.

SMITH, E. L.
1969. EVOLUTIONARY MORPHOLOGY OF EXTERNAL INSECT GENITALIA. 1. ORIGIN AND RELATIONSHIPS TO OTHER APPENDAGES. Ann. Ent. Soc. Amer. 62: 1051–1079.
——— 1970. EVOLUTIONARY MOPHOLOGY OF THE EXTERNAL INSECT GENITALIA. 2. HYMENOPTERA. Ann. Ent. Soc. Amer. 63:1–27.

SMITH, F. K.
1956. A COLONY OF YELLOWJACKETS, *VESPULA PENSYLVANICA* (SAUSSURE). Ent. News 67:141–146.

SNELLING, R. R.
1970. THE SOCIAL WASPS OF LOWER CALIFORNIA, MEXICO (HYMENOPTERA: VESPIDAE). Contributions in Science (Los Angeles County Museum of Natural History) 197:1–20.

SOBOTKA, A. K., R. M. FRANKLIN, N. F. ADKINSON, JR., AND OTHERS.
1976. ALLERGY TO INSECT STINGS. II. PHOSPHOLIPASE A: THE MAJOR ALLERGEN IN HONEYBEE VENOM. Allergy Clin. Immunol. J. 57:29–40.

SPENCER, G. J.
1960. ON THE NESTS AND POPULATIONS OF SOME VESPID WASPS. Ent. Soc. Brit. Columbia Proc. 57:13–15.

SPRADBERY, J. P.
1971. SEASONAL CHANGES IN THE POPULATION STRUCTURE OF WASP COLONIES (HYMENOPTERA: VESPIDAE). J. Anim. Ecol. 40:501–523.

______
1973a. WASPS: AN ACCOUNT OF THE BIOLOGY AND NATURAL HISTORY OF SOLITARY AND SOCIAL WASPS. University of Washington Press, Seattle. 408 pp.

______
1973b. THE EUROPEAN SOCIAL WASP, *PARAVESPULA GERMANICA* (HYMENOPTERA: VESPIDAE) IN TASMANIA, AUSTRALIA. International Union for the Study of Social Insects (IUSSI) Proc. VII Internatl. Congress, pp. 375–380.

______
1975. THE BIOLOGY OF *STENOGASTER CONCINNA* VAN DER VECHT WITH COMMENTS ON THE PHYLOGENY OF STENOGASTRINAE (HYMENOPTERA: VESPIDAE). Australian Ent. Soc. J. 14:309–318.

TAYLOR, L. H.
1939. OBVERSATIONS ON SOCIAL PARASITISM IN THE GENUS *VESPULA*. Thomson. Ann. Soc. Amer. 32:304–315.

THOMAS, C. R.
1960. THE EUROPEAN WASP (*VESPULA GERMANICA* FAB.) IN NEW ZEALAND. New Zeal. Dept. Sci. and Ind. Res. Inf. Ser. 27:1–74.

TISSOT, A. N., AND F.A. ROBINSON.
1954. SOME UNUSUAL INSECT NESTS. Fla. Ent. 37:73–92.

VAN DER VECHT, J.
1957. THE VESPINAE OF THE INDO-MALAYAN AND PAPUAN AREAS (HYMENOTPTERA: VESPIDAE). Zool. Verh. Rijksmus Nat. Hist., Leiden. 34:1-83.

______
1977. STUDIES OF ORIENTAL STENOGASTRINAE (HYMENOPTERA: VESPIDAE). Tijdschr. Ent. 120:55–75.

WAGNER, R. E.
1961. CONTROL OF THE YELLOWJACKET *VESPULA PENSYLVANICA* IN PUBLIC PARKS. J. Econ. Ent. 54:628–630.

______
1978. THE GENUS *DOLICHOVESPULA* AND AN ADDITION TO ITS KNOWN SPECIES OF NORTH AMERICA (HYMENOPTERA: VESPIDAE). Pan-Pac. Ent. 54:131–142.

______ AND D. A. REIERSON.
1969. YELLOWJACKET CONTROL BY BAITING. 1. INFLUENCE OF TOXICANTS AND ATTRACTANTS BY BAIT ACCEPTANCE. J. Econ. Ent. 62:1192–1197.

______ AND D. A. REIERSON.
1971a. RECOGNIZING AND CONTROLLING YELLOW-JACKETS AROUND BUILDINGS. Natl. Pest Control. Oper. News 31(1):6–7; 30–32.

______ AND D. A. REIERSON.
1971b. YELLOWJACKET CONTROL WITH A SPECIFIC MIREX-PROTEIN BAIT. Calif. Agric. 25:8–10.

WALTON, G. M., AND G. M. REID.
1976. THE 1975 NEW ZEALAND EUROPEAN WASP SURVEY. New Zeal. Beekeeper 38:26–30.

WEST EBERHARD, M. J.
1969. THE SOCIAL BIOLOGY OF POLISTINE WASPS. Univ. Mich. Mus. Zool. Misc. Publ. 140:1–101.

WEYRAUCH, W.
1935–36. *DOLICHOVESPULA* AND *VESPA*. VERGLEICHENDE ÜBERSICHT ÜBER ZWEI WESENTLICHE LEBENSTYPEN BEI SOZIALEN WESPEN. MIT BEZUGNAHME AUF DIE FRAGE NACH DER FORTSCHRITTLICHKEIT TIERISCHER ORGANISATION. (I. & II. TEIL). Biol. Zentralbl. 55:484–524; 56:287–301.

______
1937. ZUR SYSTEMATIK UND BIOLOGIE DER KUCKUCKSWESPEN *PSEUDOVESPA*, *PSEUDOVESPULA* UND *PSEUDOPOLISTES*. Zool. Jahrb. (Syst.) 70:243–290.

WHEELER, W. M., AND L. H. TAYLOR.
1921. *VESPA ARCTICA* ROHWER, A PARASITE OF *VESPA DIABOLICA* DE SAUSSURE. Psyche 28:135–144.

WHITE, L. D., R. B. HUTT, AND B. A. BUTT.
1969. RELEASES OF UNSEXED GAMMA-IRRADIATED CODLING MOTHS FOR POPULATION SUPPRESSION. J. Econ. Ent. 62:795–798.

WHITEHEAD, V. B., AND A. J. PRINS.
1975. THE EUROPEAN WASP, *VESPULA GERMANICA* (F.) IN THE CAPE PENINSULA. Ent. Soc. South Africa J. 38:39–42.

WILLIAMS, F. X.
1927. NOTES ON THE HABITS OF THE BEES AND WASPS OF THE HAWAIIAN ISLANDS. Hawaiian Ent. Soc. Proc. 6(3):425–464.

______
1937. EXHIBITIONS AND DISCUSSIONS OF LOCAL MATERIAL. Hawaiian Ent. Soc. Proc. 9(3):366.

WILSON, E. O.
1971. THE INSECT SOCIETIES. Belknap Press of Harvard University Press, Cambridge, Mass. 548 pp.

YAMANE, S.
1975. TAXONOMIC NOTES ON THE SUBGENUS *BOREOVESPULA* BLÜTHGEN (HYMENOPTERA: VESPIDAE) OF JAPAN, WITH NOTES ON SPECIMENS FROM SAKHALIN. Kontyû 43:343–355.

YOSHIDA, H., R. G. GELLER, AND J. J. PISANO.
1976. VESPULAKININS: NEW CARBOHYDRATE-CONTAINING BRADYKININ DERIVATIVES. Biochemistry 15: 61–64.

ZELEZNICK, L. D., K. J. HUNT, A. K. SOBOTKA, AND OTHERS.
1977. DIAGNOSIS OF HYMENOPTERA HYPERSENSITIVITY BY SKIN TESTING WITH HYMENOPTERA VENOMS. Allergy Clin. Immunol. J. 59:2–9.

APPENDIX

Glossary of Selected Terms Used in the Text

Aculeate. — Pertaining to the stinging members of the order Hymenoptera; that is, the bees, ants, and wasps.

Alimentary liquid. — Any material in the food canal of adults and larvae.

Anaphylactic shock. — A sometimes violent physiological response to the introduction of a foreign substance such as venom into the body of a person hypersensitive to that substance.

Apiary. — Any place where honey bees (Hymenoptera:Apidae) are kept.

Associate. — Arthropods (spiders, mites, sowbugs, and other insects) found in or around yellowjacket colonies and nests. Many are scavengers, a few are parasites.

Biotype. — A group of organisms having the same genetic makeup but possibly different physical characteristics.

Brood. — All the immature members of a colony including eggs, larvae, and pupae.

Cap. — A covering of silk secreted by a larva over the opening of a cell shortly before it forms a pupa.

Carton. — Material comprising the combs and suspensoria of yellowjacket nests.

Caste. — A group of morphologically distinct individuals within a colony often having distinctive behavior (that is, workers, queens, and males).

Chronologued colony. — A colony the activities of which have been recorded on a daily basis from beginning through decline to death.

Cocoon. — A silken enclosure secreted by a larva just before pupation; exposed end called a "cap."

Colony. — Individuals, other than a single mated pair, which cooperate to construct a nest or rear offspring.

Comb. — A single layer of regularly arranged cells or cocoons.

Cryptic. — Concealing or camouflaging, as in cryptically colored moths often difficult to see against their substrates.

Cyanosis. — A bluish discoloration of the skin due to inadequate oxygenation of the blood.

Discoidal cell. — A closed (surrounded by veins) cell or cells in the middle of the wing.

Dominance hierarchy. — A behavioral domination of certain members of a colony over certain other members; a "pecking order."

Duff.— Decayed leaves and branches of the surface of the forest floor.

Eclosion. — Emergence of an adult from a pupal case or cocoon.

Electrophoresis. — Migration of different substances at different rates within an electrical field, used to separate small amounts of chemical components of a mixture.

Encapsulated formulation. — Insecticide coated with a plastic material (microcapsules) causing the toxic component to release slowly.

Envelope. — Sheaths of paper or masticated plant fiber surrounding the combs of a nest.

Epinephrine. — An adrenal hormone that stimulates organs or tissues (heart rate, smooth muscle of lung, and blood vessels) controlled by the autonomic nervous system.

Eusocial. — A condition in which a group of individuals exhibits division of labor, with sterile members of the group working on behalf of actively reproducing members and with two or more generations (that is, foundress and her daughter workers) contributing to the group welfare.

Facultative parasite. — An organism capable of supporting itself (free living) but which may occasionally obtain its livelihood at the expense of another organism called the host.

Female. — In reference to polistine wasps, an overwintering, fertilized individual that cooperates with other such individuals to construct a nest; one usually becomes dominant.

Forager. — An individual colony member, usually a member of the worker caste, that searches for and obtains food, water, or building materials.

Foundress. — An individual, usually a fertilized female, that founds a colony, all the members of which would be her daughters or sons.

Gaster. — The prominent part of the abdomen, separated from the other parts of the body by a thin connecting segment called the petiole or pedicel.

Girdle. — A band made around a tree by removal of a ring of bark, usually killing the tree.

Gravid. — Full of ripe eggs.

Haplometrosis. — The founding of a colony by a single fertilized female or foundress.

Hornet. — Large wasps belonging to the genus *Vespa*, although erroneously applied to the bald-faced "hornet," *D. maculata*.

Incipient. — An initial or early stage of a colony or its nest.

Incised. — Cut into or notched.

Inquiline. — In the broadest terms, any individual occurring in the nest of another individual.

Interspecific. — Involving individuals of two or more species.

Intraspecific. — Involving individuals of the same species.

Lymphadenopathy. — An abnormal state of the lymph glands often associated with swelling of the glands.

Malaise. — A feeling of being ill or depressed.

Malaxating. — Chewing and squeezing of prey by an adult yellowjacket, which softens prey and reduces it in size before it is given to larvae.

Mastication. — Chewing and mechanically breaking up food or building material.

Mauling. — Stereotyped interaction in which one worker vigorously bites another but apparently produces no physical damage to the usually motionless recipient.

Medial. — Toward the midline of the body.

Melanic. — Exhibiting a predominance of dark brown pigmentation.

Mesonotum. — The upper surface of the mesothorax.

Nest sanitation. — A behavior pattern resulting in rapid removal from the nest of dead or dying brood, unused prey, and other debris.

Nest usurpation. — The adoption of a colony by an unrelated individual, usually by forcible eviction or death of the foundress.

Obligate parasite. — A parasitic association in which the parasite cannot complete its life cycle without the host.

Opportunistic. — Ability to accept whatever resources (food, nest, or sites) are available at the time.

Paper wasp. — Members of the genus *Polistes*.

Parasitism. — An association in which one organism, called the parasite, lives at the expense of another organism, called the host, without killing it.

Parasitoid. — A type of parasitic association in which the host is eventually killed by the parasite.

Pleometrosis. — The founding of a colony by more than one fertilized female or foundress.

Polyarthritis. — Simultaneous inflamation with associated pain of several joints.

Presocial. — A condition in which a group of individuals exhibits only one or two of the following traits: Cooperation in care of immatures, sterile members working in behalf of actively reproducing members, or with two or more generations contributing to group welfare.

Queen. — A member or an egg-producing caste as opposed to a worker caste or a male caste.

Reproductive diapause. — In the adult, a temporary cessation in ability to develop mature oocytes (eggs).

Reproductives. — Any individuals of a colony (that is, males and females capable of being fertilized) able to reproduce.

Royal court. — *Vespa* workers surrounding and licking the queen, which is highly attractive.

Scutum. — The dorsocentral part of an insect thoracic segment.

Septicemia. — A disease state caused by pathogenic organisms in the blood; often called "blood poisoning."

Social parasite. — A type of parasitism involving a social insect as host.

Species group. — A group composed of several to many closely related species.

Subcutaneous. — Beneath the skin.

Submarginal cell. — Closed cell in the insect wing, occurring just posterior to the leading edge of the wing.

Sympatric. — A condition in which several noninterbreeding populations occupy the same geographic area.

Urticaria. — An allergic reaction of the skin to foreign substances such as venom, indicated by itchiness and welts.

Ventral. — Closest to the lower surface or "belly" area of the body.

Vespine wasp. — Members of the Vespinae, including *Provespa*, *Vespa*, *Vespula*, and *Dolichovespula*.

Wall void. — space between the outer and inner walls of a building.

Wasp (that is, true Wasp). — Hymenoptera that have the ovipositor modified into a sting for injecting venom into the host. Egg no longer passes down the modified ovipositor.

Worker. — A member of a nonreproductive or sterile caste, which contributes to a colony welfare by rearing offspring of reproductives.

Xanthic. — Exhibiting a predominance of yellow pigmentation.

Yellowjacket. — Any member of the ground or aerial nesting wasps belonging to the genera *Vespula* and *Dolichovespula*.

List of Chemicals Mentioned in This Publication

Pesticide designation	*Chemical name*
Carbaryl	1-naphthyl methylcarbamate
Chlordane	1,2,4,5,6,7,8,8-octachloro-3a,4,7,7,a-tetrahydro-4, 7-methanoindan (60% minimum and not over 40% of related compounds)
Diazinon	*0,0*-diethyl *0*-(2-isopropyl-6-methyl-4-pyrimidinyl) phosphorothioate
Dichlorvos	2,2-dichlorovinyl dimethylphosphate
Heptyl butyrate	heptyl butyrate
Heptyl crotonate	heptyl crotonate
Hexadienyl butyrate	2,4-hexadienyl butyrate
Mirex	dodecachlorooctahydro-1,3,4-metheno-1*H*-cyclobuta[*cd*]pentalene
Propoxur	*o*-isopropoxyphenyl methylcarbamate
Pyrethrins	(An insecticidal constitutent of pyrethrum)
Resmethrin	(5-benzyl-3-furyl) methyl *trans*-(+)-2,2-dimethyl-3-(2-methylpropenyl) cyclopropanecar boxylate
Rotenone	1,2,12,12a-tetrahydro-2-isopropenyl-8,9-dimethoxy[1]benzopyran-6(6a*H*)-one